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THE A B C
OF BIOLOGY

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THE A B C OF BIOLOGY

BY

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PREFACE

This is a somewhat experimental book. The invitation to write it followed closely upon the acceptance, after some ten years of uninterrupted research, of a teaching post, and was accepted, in part, because it was felt that the writing of a short general account of animal biology would be not without benefit to the author. But it is hoped that the reader will gain some small advantage from this book which has at least the advantage of representing the opinions of one whose work has been carried on not only in the laboratory but also amongst living creatures in many parts of the world.

There is no subject more difficult to summarize concisely than biology. The manifestations of life are so many and so infinitely varied and so few general principles have so far rewarded man's study of this subject. Biology is far from that essential simplicity to which the physical sciences are so rapidly attaining. The one general principle which has so far emerged is the concept of evolution. Logically, perhaps, any general account of biology should be based on this, and the great majority of text-books and popular accounts of biology written during the past half-century have been essentially descriptions of the structures of animals ranging from "Amoeba to Man". There were many good reasons for this so long as the idea of evolution

was new and needed impressing upon the minds of students and the general public. But evolution is now universally accepted; it forms a part of the heritage of human thought. Biology is no longer pre-occupied, as it was during the latter half of the nineteenth century, with the description of its diverse subject matter and the fitting of this into the evolutionary tree. It has once more become, as it was in the eighteenth and early nineteenth centuries, an experimental science. The study of function has re-joined hands with the study of structure and to the inestimable advantage of both.

Any modern account of biology must, therefore, treat it as an experimental science. The various manifestations of life must be regarded as no less suitable for experimental analysis than the subject matter of chemistry and physics. At the same time biology is something more than bio-chemistry and bio-physics, than the application of the methods of chemistry and physics to the analysis of living matter. There is a biological point of view which is broader and deeper than the purely physiological point of view, although it must include this. It is impossible fully to explain the animal or the plant as a whole by the analysis, no matter how detailed, of the constituent parts. It is necessary, therefore, to follow the description of the mechanisms of living matter with an account of the organism as a whole.

There remains the consideration of the organism as a unit in Nature, and of the part every plant and every animal plays in the economy of Nature. These three

main sub-divisions are preceded by a short account of the essential characteristics of living matter and of the factors which condition it, with some surmises as to its possible mode of origin, and are followed by a short epilogue in which, should the reader penetrate so far, he will find a brief statement on modern tendencies in biological thought.

Owing to the great diversity of living things any account of biology must be largely descriptive and it is for this reason that references to the plant kingdom, a full account of which would demand more space than is here available, have been confined to the general account of living matter and to a description of the interactions between plants and animals. The latter, therefore, constitute the real theme of this book. As many different types as possible have been considered, the intention being to emphasize alike diversity in form and yet fundamental similarity.

Many of the particular examples chosen, notably in the later sections, deal with marine life to which the author's original investigations have been confined. This calls for no apology ; life probably arose in the sea in which still dwell by far the greatest diversity of living things, while of what should one write better than of the things which interest one the most ?

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Bristol.

January, 1934.

CHAPTER I

THE NATURE AND ORIGIN OF LIVING MATTER

THE Universe is composed of matter which may broadly be divided into the non-living and the living. The distinction between these lies not in their actual composition, for both are composed of the same elements, but in the unique properties of living matter. Of these the most obvious are feeding, growth and reproduction, but living matter may probably best be defined as matter capable of self-regulation. Although the most complex form of matter, or of stored energy, it exists in a state of continual but somewhat unstable equilibrium both with its constituent parts and with the external world. As both internal and external conditions are continually changing living matter must be capable of simultaneous accommodation. In other words it must have the power, characteristic of life alone, of irritability. It must be capable of receiving impulses and of so reacting to them as to persist. Should it fail to do so the power of self-regulation is lost and it ceases to be living matter.

Non-living matter is immensely more abundant than living matter. True, the greater part of the land area of this planet is clothed with vegetation which supports a diverse fauna while the oceans teem with life of every kind, but only a very small proportion of other worlds can conceivably support life. The stars,

which correspond to our sun, are much too hot, the number of planetary systems, such as the one to which the earth belongs, is small and on only a very few of these planets is life possible. It is all a matter of temperature. If the planets are too near to the stars around which they revolve the temperature will be too high, if they are too far away it will be too low. Moreover, as the heat of the stars declines life will gradually become unsupportable on more distant planets and gradually become possible on nearer ones. In the present condition of the sun the earth is at just the right distance from it to receive the appropriate amount of heat for life; Mars may well have had life upon it, if so this is probably now on the decline; after the wane of life on the earth it may be the turn of Venus, the planet immediately nearer to the sun. It does not, of course, follow that life has developed on Mars or will develop on Venus, but there are no known physical reasons against this. But clearly at best living matter must be confined to a minute fraction of the universe, according to Sir James Jeans to no more than one thousand million millionth part of the whole of space.

A certain range of temperature is essential because protoplasm, the name given to the actual substance of living matter, is very unstable and can only exist as living matter in temperatures ranging between about − 2 degrees C. and 35 degrees C., although there are a few rare exceptions to this, notably the bacteria which live in hot springs in New Zealand.

A certain and very restricted range of temperature is but one of a number of physical and chemical factors

which have controlled or made possible the appearance of living matter. Of these the unique properties of water must take first place. While occasionally rendering lip service to this life giving fluid we are apt, by reason of its very ubiquity, to take for granted this most remarkable substance. Water is imbibed and excreted by living matter more freely than any other substance, water is perpetually streaming through the bodies of all living organisms which are actually largely composed of it, from 70 to 95 per cent of protoplasm being water. Living matter actually exists in aqueous solution.

Water is the most perfect of solvents, but it is also, because of the great affinity of its constituent elements, hydrogen and oxygen, chemically very inert; it does not readily attack other substances. Held in this vehicle of water the many constituents of living matter are able to react readily with each other without affecting or being affected by the fluid in which they are dissolved. Water, moreover, has a very high dielectric constant, by which we mean that it has an unusual capacity for keeping apart the constituent elements of many of the compounds which dissolve in it, and which under such conditions take on an electric charge and are known as ions. Matter in this form is extremely active and many of the most essential processes of life are carried out through the intervention of ions, which have a profound effect on the colloidal state in which living matter exists.

Again the thermal properties of water are unique. Its specific heat is very high. This means that a

relatively large amount of heat is necessary to raise the temperature of water. The value of this property to living matter is obvious, for it contains a high proportion of water and can only exist within certain temperature limits. The high specific heat of water is one of the reasons why the temperature of lakes and oceans is so remarkably constant compared with the land, since so great an amount of heat must be absorbed before the temperature of the water rises appreciably. This was probably of fundamental importance in the origin of life and is certainly a vital factor in the maintenance of aquatic life.

The latent heats of melting and evaporation of water are of similar significance in the origin and maintenance of life. By these terms are meant the amount of heat needed to convert a definite amount of ice into water or water into vapour. The latent heat of melting of water is almost the highest known while that of evaporation is by far the highest. Here again are most potent mechanisms for the maintenance of constant temperature. The evaporation of water absorbs so much heat that the tropical oceans are kept relatively cool owing to the direct utilization of heat rays from the sun in the process while in the evaporation of perspiration from the surface of our own bodies we have an excellent example of the direct utilization of this property of water by living organisms. The high latent heat of melting ensures that ice is only formed with considerable difficulty, moreover, however low the temperature drops the actual temperature of the mixture of ice and water cannot fall below 0 degrees

C. until the whole of the water has been turned into ice, and life at this temperature is still possible. Of equal significance in this connection is the well-known property, possessed by water alone, of expanding before freezing. All other liquids as they are cooled become denser and denser until finally they solidify. Water behaves in a similar manner until the temperature reaches 4 degrees C. below which it gets lighter. In consequence water below this temperature tends to rise and float on the surface of warmer and heavier water and so the formation of ice invariably occurs from the surface downwards. Were it not for this ice would begin to form on the bottoms of lakes and oceans and the whole of the water might freeze in the winter, so that even the heat of the summer would fail completely to dissolve the ice and until that had happened the temperature of the water could nowhere rise above 0 degrees C. Life under such conditions would probably speedily become impossible not only to organisms living in water but also on land for the oceans might finally freeze solid with a consequent disastrous drop in air temperature.

There is a second, very simple chemical compound of equal importance to life but which must be considered after the water through solution in which it exerts much of its influence. This is carbon dioxide (CO_2) or carbonic acid gas. It is by way of this gas that the element carbon, the veritable rock on which all life is built, has been and continues to be incorporated into living matter. Carbon dioxide possesses the unique property amongst the gases of the atmosphere of being

present in almost equal proportions in the atmosphere and in solution in water. It is thus always available for life in either medium while it passes from the one to the other with perfect ease so that any lack of it in the one medium can be made good by diffusion from the other. When carbon dioxide dissolves in water it forms the very weak carbonic acid which interacts with bases to form salts known as carbonates and bi-carbonates, such as sodium carbonate, Na_2CO_3 and sodium bi-carbonate, $NaHCO_3$. Now these substances are of vital importance both in the oceans and also in the body fluids of animals, in maintaining the condition known as neutrality. This can best be described as the counter-balancing of the hydrogen and hydroxyl ions, H and OH, which when in excess the one over the other are responsible respectively for the conditions known as acidity and alkalinity. So long as water is neutral it is chemically inert which, as we have already seen, is one of its essential properties as a medium, external or internal, of living matter. If water becomes acid or alkaline it becomes chemically active and life speedily becomes impossible. Actually both in the sea (though not to the same extent in fresh waters) and in the interior of protoplasm or living organisms this hydrogen ion concentration is kept remarkably constant and near to neutrality. This is almost entirely the result of the so-called 'buffering' action of bi-carbonates and carbonates which in turn is rendered possible by the ubiquity and also the weak acid properties of carbon dioxide.

A consideration of the rôle played by carbon dioxide leads us logically to the chemistry of living matter.

Although protoplasm is by far the most complex substance known, it is formed from comparatively few elements of which carbon, hydrogen and oxygen are much the most numerous and important, followed by nitrogen, phosphorus, calcium, sulphur and a variety of other elements the importance of which may, as we shall see later, be out of all proportion to the actual amount present. Living matter is built up around carbon. This element is what is known as quadrivalent which means that one atom of carbon can combine with four atoms of a univalent element such as hydrogen (forming methane, CH_4), or with two atoms of a divalent element such as oxygen (forming carbon dioxide, CO_2). The carbon atom forms the basis of an unlimited number of compounds. Its atoms have the unique power of forming long chains (more than sixty may be present in a single chain) or rings composed of six atoms. These are the skeletons to which other elements are attached, and they are capable of endless complications, the chains may branch in many different ways while side chains may grow out from rings which may also be united with one or more other rings. The principal element attached to carbon is always hydrogen, indeed the properties of carbon are inextricably mingled with those of hydrogen. Where hydrogen alone is present we have a great group of substances known as the hydrocarbons, the great natural sources of which, coal and oil, are formed from the fossilized bodies of organisms.

When oxygen is present as well as hydrogen a much greater range of substances can be formed, many of which are amongst the most important constituents of

living matter. Chief amongst these are the sugars, which are members of the great group of substances known as carbohydrates (because in them oxygen and hydrogen are present in the same proportions as in water), the fats, organic acids of all kinds such as acetic acid, lactic acid, oxalic acid, citric acid and so forth, the great group of the alcohols (which include glycerine), acetone, ether and innumerable other substances with all manner of different chemical properties.

Complex with the addition of hydrogen alone, much more so with the further addition of oxygen, the addition with these of still further elements to the skeleton of carbon produces an even more varied array of compounds including some of such intricacy of structure that chemists are still uncertain as to their exact composition. These latter are the proteins in all of which nitrogen is present as well as carbon, hydrogen and oxygen, and also often other elements, notably phosphorus and sulphur. The protein molecule is, chemically speaking, of immense size and may contain more than one thousand atoms. The proteins are the most characteristic constituents of living matter which is inconceivable without them.

The study of the compounds of carbon is known as organic chemistry because it was originally thought that these substances could only be formed by living matter. This view received its death blow in 1828 when a German chemist named Wöhler prepared or 'synthesized' in the laboratory the organic compound urea which is very frequently found in living matter. Since that date many other 'organic' compounds

have been similarly prepared including those of such complexity as cane sugar and some amino-acids (large aggregations of which form the protein molecule). There can be no doubt that eventually the proteins themselves will be prepared in the same way.

Living matter then has as its ultimate chemical basis the element carbon upon which can be built up innumerable substances (over half a million organic compounds have been isolated or prepared up to the present and this number is capable of indefinite addition). These range in complexity from carbon dioxide, with its three constituent atoms to the proteins with their thousands and include substances of every possible description; solids, liquids and gases; acids and bases; stable, inert substances and unstable, highly active substances. It has already been stated that living matter is characterized by a perpetual need for activity of one kind or another in response to stimulation from within or without while it is also being simultaneously built up and broken down. The instability of many of the organic compounds present in living matter provides the energy so continuously needed while the presence on the other hand of more stable substances, such as the proteins, provides for the stability of the whole. Organic compounds constitute ideal chemical sources of energy. This is obtained by living matter in two ways. Complex substances may be split up into simpler ones, thereby releasing the energy which was originally utilized in their formation and has since been locked away within them. This process is known as fermentation and is of widespread occurrence in bacteria and in

yeasts. The classic example of a ferment is the zymase found in yeast which splits up grape sugar or glucose ($C_6H_{12}O_6$) into alcohol (C_2H_6O) and carbon dioxide. Fermentation was aptly described by Pasteur as " life without oxygen " and, as we shall see, there is good reason for regarding this as the primitive method of obtaining the energy necessary for life.

In animals and higher plants energy, with rare exceptions, is always obtained by oxidation, which explains the almost universal need for oxygen amongst living things. In some chemical reactions energy, normally in the form of heat, is absorbed, in others it is liberated. No reaction absorbs so much heat as the ' reduction ' of a compound, a process which involves the removal of oxygen, and no reaction liberates so much energy as oxidation, or the addition of oxygen to any substance. Moreover when the elements are arranged in order according to the amount of energy produced when they are oxidized, hydrogen comes first in the list and carbon third. Living matter, so rich in compounds of carbon and hydrogen, and surrounded with abundant oxygen, either in the atmosphere or in solution in water, has at its disposal a most potent source of energy.

These are some of the more important of the factors which have made life possible but which at the same time have hedged it around with restrictions. Living matter has not been content to accept without a struggle the domination of physical forces and the story of organic evolution is the story to a large extent of the successive triumphs of living things over the forces of the

environment. But the ultimate dependence of living matter on the physical and chemical properties of its constituent matter must always remain. It is impossible to conceive of life in the absence of these.

In appearance protoplasm is a transparent, semi-fluid substance which usually contains granules of various kinds. Even when these are apparently absent, observation under the high powers of the microscope reveals that protoplasm is far from being a homogeneous substance. It is actually, regarded purely from the chemical aspect though it must be remembered that as soon as it dies its properties immediately alter, a very elaborate colloidal system. This implies that the proteins and the fats which form the bulk of protoplasm and which cannot, like the majority of the sugars or inorganic compounds, pass into true solution, exist instead in a kind of suspension in the watery medium which forms the vehicle for protoplasm. Substances capable of such permanent suspension are known as colloids. Colloid chemistry is a recent but very important branch of science and it teaches us, amongst other things, that the many remarkable properties possessed by colloidal solutions are due in the main to the great surface exposed by the large molecules or aggregations of molecules which lie in suspension. These surfaces, owing to the electric charges present on them and also to that property of liquids known as surface tension, are the site of intense chemical activity. The highly intricate colloidal structure of protoplasm renders possible the unending series of chemical reactions characteristic of living matter.

It may be of help at this stage in the description of the characteristics of living matter if a short account be given of the manner in which this *may* have originated. This is, of course, a matter for conjecture—the true story must await the discovery not only of the exact nature of living matter but also of the manner in which this can artificially be prepared, and neither of these is even remotely in sight. But our guesses as to the origin of living matter, reflecting as they do current ideas as to its nature, are not without help in the understanding of the problems of life.

We know from spectrascopic examination that the atmosphere of hot stars is particularly rich in hydrogen and that as they begin to cool carbon appears in great quantities. There is also every reason for assuming the presence of unlimited oxygen. In white hot stars all matter exists in the form of elements but as the temperature drops chemical combination becomes possible. The great affinity between hydrogen and oxygen and carbon and oxygen must result in the appearance of vast quantities of water vapour and carbon dioxide in the atmosphere of cooling planets. There is much to be said for the view that in the case of the earth, where we have most evidence to work upon, all the oxygen was utilized in the formation of these substances and that the primitive atmosphere was devoid of this gas. As the earth cooled still further and a solid crust was formed the water vapour would gradually condense as liquid upon its surface and in course of time give rise to the primitive oceans. The first substances to be dissolved in quantity in this would

be carbon dioxide from the atmosphere and probably to a less extent ammonia (NH_3), formed possibly by the interaction of water on certain nitrogenous compounds in the crust of the earth. The slight acidity given to the water by the presence in it of carbonic acid would be of assistance in the collection within itself by solution to a greater or less extent of all the elements in the earth's crust.

We now have water containing abundant carbon dioxide, ammonia and a steadily increasing concentration of other inorganic compounds. The stage is now set for the building up of more complex organic compounds which must have been the first act in the titanic drama which, by way of the appearance of more and more complex substances and more and more complex union between these, culminated in the appearance of living matter. The energy needed for the formation of complex from more simple substances came from the sun which was, is and must always be, the motive power behind all life. At that time when they reached the surface of the earth the sun's rays probably contained many more of the extremely active ultra-violet rays than is the case to-day. The absence of oxygen from the atmosphere at that time prevented the formation of the blanket of ozone (O_6) which apparently largely absorbs these rays at the present time. There is certain experimental evidence that under such conditions sugars and other complex organic compounds would be formed while, in the complete absence of the decay due to bacteria which would not be evolved for many million years, these would accumulate until, in the

words of Professor J. B. S. Haldane, " the primitive oceans reached the consistency of hot dilute soup ".[1]

Although there is no further experimental evidence to help us, we may envisage the next stage as the formation of larger and yet larger molecules which eventually acquired—how, we do not know—some of the characteristics of living matter. They became able to maintain their complex and inevitably unstable organization by some process of repair which would offset that of breaking down. This might come about by means of that surface activity to which reference has already been made. Then they must have acquired the power of growth and reproduction. There is an analogy to the former process in the growth of crystals but the development of the latter is more difficult to envisage. It may at first have been possible only under certain especially favourable conditions for something of the same sort seems to occur in the bacteriophages which destroy bacteria and which, if they are actually living matter, are the smallest known organisms.

In some such manner the first living matter may well have been formed, obtaining its energy, oxygen being still absent, by fermentation, and feeding by incorporating within itself the organic matter so abundantly present in the oceans. In time this source of food would be exhausted, and then, or earlier, living matter must have begun to obtain its food direct from

[1] The reader is referred to Professor Haldane's striking essay on " The Origin of Life " in his book *The Inequality of Man* to which I am glad to be able to express my indebtedness.

the simplest constituents, carbon dioxide, water and inorganic salts. For this the energy of sunlight was needed so living matter which lived near the surface of the sea could alone develop this power. In this way the first plants were formed for it is the essential distinction between plants and animals that the former alone can feed on inorganic matter, and so build up organic matter from its simplest constituents. This they do by the action of their green colouring matter, chlorophyll, which, in the presence of the radiant energy of sunlight, is able to form starch (a complex sugar) from carbon dioxide and water. Chlorophyll is the most important substance in the world of living matter. The majority of organisms, including the whole of the animal kingdon, which do not possess it are completely dependent for their food on those which do. The first appearance of chlorophyll, or rather of its original progenitor, for it is an extremely complicated compound, forms one of the great landmarks in the evolution of living matter. The reappearance of oxygen, assuming that the primitive atmosphere was devoid of this element, must have been one of the consequences of the first appearance of chlorophyll. When starch is formed by chlorophyll in the process of photosynthesis oxygen is invariably liberated. It was living matter, utilizing the energy of sunlight, which first separated it from its original combination with carbon and hydrogen.

The consequences of the appearance of oxygen in solution in the water and free in the atmosphere would be profound. Living matter was now able to avail itself

of the most potent form of energy, that of oxidation, and largely abandoned the less efficient method of fermentation. This is still used, as we have seen, by certain simple forms of life, indeed certain bacteria cannot even exist in the presence of oxygen—they are what is known as anaerobic in contradistinction to organisms which live in oxygen and are called aerobic—and though these may be degenerate it is just possible that they do represent a survival from a very early stage in the evolution of life.

It is a long step from such hypothetical forms to living matter as it exists at the present time, including animals and plants of great size and intricacy of organization. Our consideration of these must begin with a description of the living cell, which is often described as the biological unit; actually though a unit of structure it is seldom a functional unit. In the year 1665 one of the early microscopists, Robert Hooke, examining a section through a piece of cork, saw that this was composed of little box-shaped compartments, which he called cells. Much later, in the middle of the last century, it was stated by Schleiden and Schwann that all protoplasm is divided up in this way. This was the origin of the cell-theory of living matter. The name cell is unfortunate, though an apt enough description of the non-living woody tissue with empty cavities examined by Hooke, for it draws attention to the walls rather than to the contents. A cell may be defined as a small mass of protoplasm consisting of a central nucleus surrounded by cytoplasm which is bounded by a cell-membrane.

A glance at Figure 1 will assist in the understanding of these terms. The mass of the cell consists of cytoplasm, the name given to protoplasm as distinct from the nucleus. This frequently contains granules of reserve food material. The nucleus, typically situated

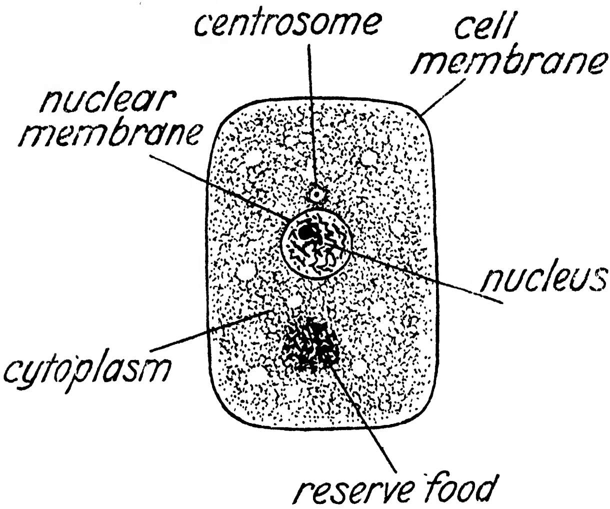


Fig. 1.
Diagram of a generalized cell.

in the centre of the cell, is a small, rounded body very clearly separated by a nuclear membrane from the surrounding cytoplasm. When living little structure can be distinguished within it, but by appropriate staining methods a meshwork of fine fibres, known as linin, can be distinguished lying in a more fluid nuclear

sap. In the linin threads are suspended masses of chromatin, so-called because after death it stains very easily. In the more complex plants and animals this chromatin coalesces to form the all-important chromosomes which will be discussed in detail later. In the bacteria, sometimes regarded as very degenerate forms of life but which may quite possibly be very primitive, there is no separate nucleus but chromatin granules are scattered throughout the cytoplasm.

The cell-membrane, except where, as in the plants, it forms round itself woody tissue, is inconspicuous but of fundamental importance. It appears to consist of a complex of proteins and fats and, although freely permeable in water it forms an effective barrier against the entrance of the majority of substances which dissolve in water. In this way the diverse activities of the contained protoplasm are sheltered from outside interference, nutrient and other essential substances alone being allowed ingress and waste matter egress. The chemical activities of the cell are probably controlled to a large extent by the nucleus which is itself the chief centre of this activity—the region of liberation of energy in contrast to the cytoplasm where it is largely accumulated. It is possible, by very delicate manipulation, to cut cells and it has been found that a fragment containing a nucleus will continue to live under appropriate conditions whereas cytoplasm without a nucleus invariably dies.

Cells are invariably very small, ranging in diameter from 0.005 to 0.05 millimetres. The great exception are egg cells which are fundamentally different from

ordinary cells and may contain enormous masses of yolk for the nourishment of the developing embryo as in the eggs of birds. Cells increase by division and the growth of organisms is due to this. A single nucleus can apparently only control the activities of a limited amount of cytoplasm and when this is exceeded the cell divides. This involves the division of the nucleus. This is occasionally direct, i.e., the nucleus elongates, becomes constricted in the centre and then breaks in two, but is more usually indirect by the elaborate and characteristic process known as mitosis. This can more suitably be described later (p. 122), but it should be clearly understood at this stage that every cell has been produced by some pre-existing cell and every nucleus by some pre-existing nucleus; that there is, in short, a definite continuity of cells, of nuclei and of protoplasm generally.

Living matter as it exists to-day is divisible into two great groups, the plant kingdom and the animal kingdom. The fundamental distinction between these lies, as already indicated, in their mode of feeding. By the process of photosynthesis the majority of plants form sugars out of water and carbon dioxide, this is readily converted into fats while a more elaborate synthesis, in which nitrogen and usually certain other elements are added, results in the formation of proteins from sugars. Animals have no such powers; they can only assimilate organic matter—sugars, fats and proteins—and are thus utterly dependent on plants. All flesh is grass; animals feed either directly on plants or else on other animals which have fed on plants. Two

groups of plants, the fungi and the bacteria (if the latter are regarded as plants and it is an open question), do not possess chlorophyll. The former obtain their food from decaying organic matter, so they also are dependent on green plants although they can utilize simpler compounds than can animals. The bacteria obtain nutriment in all manner of ways and they play an inconspicuous but extremely important part in the economy of life as a whole. Some obtain their carbon direct from carbon dioxide without the aid of chlorophyll, others accomplish the extremely difficult task of utilizing nitrogen from the atmosphere, others again, as we have seen, live in the absence of oxygen and obtain energy by the fermentation of organic compounds.

Each plant, each animal, every living thing, is an organism, that is its various parts co-operate, the whole constituting a single, self-regulative individual. It is the organism rather than the cell which is the biological unit. Organisms, whether plant or animal, can be sub-divided into unicellular, or, better, non-cellular organisms and multicellular organisms. In the former group, which includes the Protophyta amongst plants and the Protozoa amongst animals (together known as the Protista), the entire organism is bounded by one cell-membrane. In the majority a single nucleus is present, but in others which are larger there may be comparatively large numbers. Despite the minute size of many of these each is equivalent, essentially, to the largest plant or animal which exists. Each one is an organism capable of performing all the essential functions of living matter. At this stage in organization the

distinction between plants and animals is sometimes very poorly defined. In a group known as the Flagellates, owing to their possession of a long whip-like process called a flagellum, some individuals have chlorophyll and so are able to feed like plants but can also ingest organic matter like animals. It is the opinion of many biologists that in some such group both plants and animals find a common origin.

The multicellular plants and animals, the Metaphyta and the Metazoa, must have sprung from non-cellular ancestors. Their bodies are composed of immense numbers of cells but there is a very important distinction between these cells and the organisms frequently described as unicellular. The latter are complete organisms and the former merely parts of an organism. The cells of a multicellular organism are specialized for some particular purpose and have lost the other functions of which every cell, as a portion of living matter, is potentially capable. This matter will be dealt with in more detail when we come to the subject of development. This specialization of cells leads to the formation of tissues each with a distinct function of its own. These tissues, of which muscle, nerve, bone, cartilage, and even blood corpuscles, are but a few examples, were known to biologists long before the invention of the microscope enabled them to discover that each is composed of great numbers of highly specialized cells.

Multicellular organisms may have arisen from the non-cellular organisms in one of two ways, by the aggregation of large numbers of these which entered

into functional connection with each other, or by the splitting up of the larger, multinucleated types by the formation, within these, of cell-membranes. It is more than probable that the sponges, a primitive group of animals the constituent cells of which will come together again and largely rearrange themselves after they have been separated by straining through fine silk, have evolved in the former way. The other multicellular animals and the plants may have originated in a similar manner but it is at least possible that they have done so in the alternative manner.

Biology may be divided into morphology and physiology, the study of structure and the study of function. But such a division, though often necessary for descriptive purposes, is more apparent than real. Modern physics teaches us that matter and energy are one and indivisible. The facts of biology can never rightly be understood until it is realized that, like matter and energy, structure and function are but different aspects of the same thing. The one is meaningless without the other. One of the most instructive stages in the history of biology is the attempt at the beginning of the nineteenth century to found a science of pure morphology. It failed as it was bound to do, but the separation between structure and function still to a large extent persists. One of the objects of this book is to destroy such distinctions.

Hitherto we have been concerned with the properties common to plants and animals and with the fundamental distinctions between these two types of living matter. Space now compels that we confine attention in the

main to animal biology. This, since we are ourselves members of the animal kingdom, concerns us more closely, but it must not be forgotten that the more simply organized plants, on which animals are in a very real sense parasitic, are the more fundamental type of living matter.

Chapter II

THE MECHANISMS OF LIFE

I Accumulation of Energy

Living things are in a perpetual ferment of change. Matter is continually being taken in and built up into more complicated substances by addition and rearrangement of elements while at the same time other matter is being broken down. In other words energy is being simultaneously accumulated and dissipated. Although in form the organism does not change from one moment to the next, it is actually never for two moments the same. These energy changes are known collectively as metabolism. Those associated with the accumulation of energy are anabolic, those associated with its liberation and the production of waste matter which this involves are catabolic.

The constant demand for matter, or rather energy, which metabolism involves is met by the provision of food and oxygen—of potential energy and the means of its liberation by the process of combustion (for oxidation is a slow form of burning). The law of conservation of energy applies equally to living and non-living systems which implies that living matter has no sources of energy peculiar to itself, the amount of energy produced by any organism, in the form of work or heat, is exactly equivalent to the amount of energy taken in.

In green plants where energy from sunlight is stored in organic compounds the organism does not need to search for the constituents of these which are present in the atmosphere around its shoots and in the soil around its roots. Animals, on the other hand, must either actively search for the organic matter from which alone they can obtain energy or else develop some means of actively drawing this towards them. From the fundamental, but less obvious, difference between animals and plants have sprung all the secondary, but much more obvious, differences. Animals need mechanisms for securing food, digestive systems for converting this into a form in which it can be incorporated within the organism, organs of locomotion are necessary to enable them to search for food, or flee from other animals which seek to feed upon them, and, as a direct consequence of this, sense organs and a nervous system have developed. All of these, apparently fundamental, properties of animals are actually due to this dependence of animals upon the energy secured and stored by plants.

It is fitting, therefore, that the study of the mechanisms of living animal matter should begin with a consideration of feeding and digestion, the provision of potential energy, and of respiration, the collection and utilization of the oxygen necessary for the liberation of this energy.

Crude food consists of living plants, living animals, their dead bodies, or of organic matter derived from the latter. Its collection by animals takes many forms dependent on the nature of the food. The simplest

forms of unicellular animals, such as *Amoeba* (see Fig. 21, p. 76), possess the simplest type of feeding mechanism. The food which consists largely of still smaller organisms is engulfed directly by the protoplasm. Other Protozoa which feed on finely divided food possess elaborate mechanisms for its collection consisting of systems of fine hairs or cilia (see p. 81) the rapid beating of which creates water currents in which the

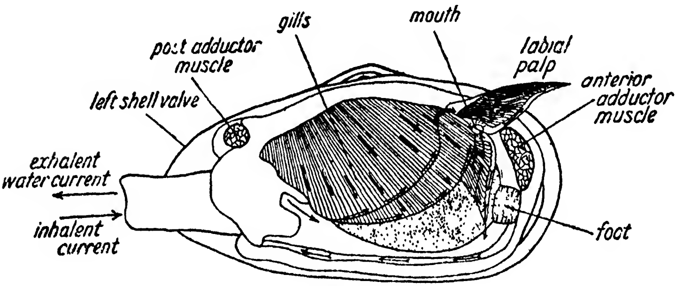


Fig. 2.

Structure of the clam, *Mya*, as revealed when the right shell valve is removed, to show the feeding mechanism of a typical bivalve mollusc. Water with suspended food material is drawn in as an inhalent current, and is then sifted through the gills, the water being passed out again as the exhalent current and fine food particles carried towards the mouth. The labial palps sort the food, allowing only the finest particles to pass to the mouth, the remainder being rejected. All currents and movements of particles are brought about by ciliary action, the direction of the principal currents being indicated by arrows (after Yonge).

microscopic food particles are carried to the mouth. This mode of feeding is very common amongst aquatic animals and is seen in its highest development in the bivalve molluscs of which the oyster and the clam (Fig. 2)

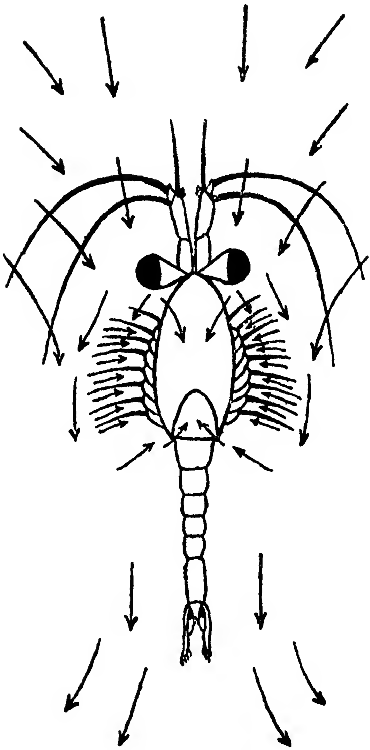


Fig. 3.

Hemimysis, a small marine crustacean, to show the currents created during movement. Water with suspended food is drawn in on either side of the body by the action of the appendages and passes to the under side of the body where the food is sifted out by means of bristles (after Cannon and Manton).

are well-known examples. The same end result is obtained by many of the smaller crustacea[1] (the great group to which the shrimps, crabs, and lobsters belong) by means of fine bristles which clothe their numerous appendages. Even the baleen whales, which include the largest of living creatures, feed by straining the minute forms of marine life from the water which rushes continually through their open mouths.

Certain animals, such as the earthworms and many marine worms, obtain food by swallowing great quantities of soil or bottom mud from which they extract any digestible matter. Others scrape their food, as do snails and their allies which possess a horny tongue or radula used for this purpose, or else are able to bore through the shells of other, usually sessile or sluggish, animals, and feed on the flesh within. The sessile sea anemones and corals and their unattached allies the jellyfish are, despite their apparent inoffensiveness, exclusively carnivorous animals which capture by means of long, extensile tentacles other animals which chance to blunder against them and which are immediately paralysed by the sting cells with which the tentacles are armed.

The majority of carnivores are definitely predacious. They possess organs of locomotion which enable them to overtake their prey and suitable organs for seizing and overpowering it. The most familiar examples of such animals are cats and dogs which run after smaller animals capturing and rending them with their jaws which possess teeth especially suited for the tearing

[1] See page 199 for outline classification of the Animal Kingdom.

of flesh. Lions and tigers, bears, wolves and seals, all feed in essentially the same manner. Reptiles, such as snakes and crocodiles, usually pounce suddenly upon animals which have approached them unawares and their teeth are adapted for seizing rather than tearing their prey which is often swallowed whole. The vast majority of fish possess teeth with which they grasp or bite pieces out of their prey but they seldom masticate their food. Octopus, cuttlefish and squids are capable of rapid darting movements and possess in their long tentacles armed with powerful suckers admirable instruments for the capture and over-powering of the living animals on which alone they feed. After their capture they tear them open with their parrot-like beaks and squirt digestive juices over them.

Finally there are parasites which live by sucking the blood or soft tissues of other animals. The flea and the mosquito are examples only too well known and, like all animals which feed in this way, they have the means for first piercing the skin of their victims and then for sucking their blood. Many parasites live actually within the body of their victim or ‘ host ’, usually either in the alimentary canal, or in the blood stream. Tape worms and the malarial parasite are good examples. In such cases organs of feeding and digestion may be entirely absent, the parasite living in a nutrient medium and absorbing food, already digested by the host, through the general surface of its body. Just as the complexity of the free-living animal is largely due to the necessity for the capture and digestion of food, so in parasites where this need is absent there

is a corresponding lack of complexity and feeding and digestive systems, organs for movement, sense organs and nerves, are all either absent or very poorly developed.

After food has been obtained it is usually passed into the digestive system. Except in parasites where this may have been lost or in non-cellular animals where, in the absence of cells and tissues, it is passed into the actual cytoplasm, the digestive system or gut consists of a cavity within the body of the animal. It consists of a tube, food entering by the mouth at the front end of the animal and indigestible matter being rejected at the anus which is usually, though not always, at the hind end. In certain cases, such as the sea-anemones and all their allies, the gut has only the one opening known as the mouth but actually serving also as an anus.

Like the feeding mechanisms, the digestive system varies greatly according to the nature of the food. Considerations of space compel us to confine attention to conditions in man which are largely typical of those in the mammals, and not greatly different from those of all the vertebrates. The most anterior region of the gut, the mouth or buccal cavity, is concerned with mastication. Here the food is mechanically divided by the grinding action of the molar teeth (the incisors and canines are used for cutting and seizing respectively). The process of swallowing which follows is assisted by the saliva poured out by three pairs of glands which moistens the food and also initiates digestion. Food then passes down the straight gullet or oesophagus

into the stomach. This is a large bag concerned essentially with the initial stages of digestion. Digestive juices and acid are produced by glandular areas in its walls and the food is thoroughly mixed with this by continuous muscular contractions of the entire stomach. After a definite period—from one to four hours in man—the pyloric valve which guards the hinder opening of the stomach and which has hitherto remained tightly shut, opens and the half-digested semi-fluid mass is squirted into the next and longest region of the gut, the small intestine. The first section of this is called the duodenum and here are the openings of the pancreas, or sweetbread, and the liver. The former is the chief digestive gland, but the liver also produces secretions essential to digestion, and the juices produced by these two and also by the walls of the intestine itself enable digestion to be completed. Absorption takes place through the wall of the small intestine and surface of which is greatly increased by numerous fine projections called villi. The small intestine in vertebrates or the corresponding absorptive region in other animals is always much longer in herbivorous than in carnivorous animals. If frog tadpoles from the same batch of eggs are fed some on meat and others on vegetable matter the former will develop much shorter intestines. This is but one example of the manner in which the form of the digestive system is influenced by the type of food, being due in this case to the much higher concentration of digestible matter in animal food. The last region of the gut in man is called the large intestine or rectum.

It is short and is concerned essentially with the accumulation and concentration, by the absorption of water, of the undigested matter. This is known as the faeces and is ejected by way of the anus.

In man, as in all the vertebrates, food is propelled through the gut by rhythmical contractions of its muscular walls, a process called peristalsis. In other animals ciliary action (see p. 81) may take the place of peristalsis or there may be a combination of the two.

Before proceeding to the actual process of digestion, the chemical nature of the food must be discussed. Food consists of three main types of substances, proteins, carbohydrates and fats. In addition small quantities of certain inorganic salts and of the all-important vitamins are absolutely necessary. Many other substances are contained in the material actually swallowed but only the first three can be digested, the others, together with water, diffusing through the walls of the gut. Not even every type of protein or carbohydrate can be utilized. For instance the complex protein called keratin which forms hoofs and hairs is indigestible as, with the exception of a few animals such as the snail, is cellulose, the complicated carbohydrate which constitutes the primary strengthening material in the body of plants.

Digestion is the conversion of proteins, carbohydrates and fats into a condition in which they can be absorbed by the walls of the intestine and so incorporated in the tissues of the animal. This conversion, or digestion, is the work of enzymes produced by the various digestive glands. These very important

substances occur everywhere in living matter which alone produces them. They may best be described as chemical lubricants. They greatly accelerate chemical reactions without themselves being appreciably affected. A very small quantity of enzyme can facilitate the conversion of large quantities of one substance into another. For instance the enzyme invertase which converts cane sugar into grape sugar (glucose) can transform over one million times its own weight of one form of sugar into the other with but little loss of efficiency. Despite much research little is known of the actual chemical nature of enzymes and it will probably be many years yet before they are artificially prepared. They are very complex, colloidal but, though usually associated with proteins, not protein in nature. Like all colloids they are very susceptible to changes in hydrogen ion concentration and will act only within a certain limited range of this. Thus the enzyme pepsin which initiates protein digestion in the stomach acts only in a very acid medium, i.e. in a high concentration of hydrogen ions. Trypsin, on the other hand, which carries protein digestion a stage further, acts only in the much more alkaline conditions present in the duodenum and small intestine. Enzymes are also very unstable and are usually destroyed at temperatures above about 50 degrees C. They are capable of promoting chemical reactions with equal facility in either direction and so are concerned with both the breaking down and building up of substances, digestive enzymes being confined of course to the former process. They are of fundamental importance in

metabolism, alike in anabolic and catabolic processes.

Although digestive enzymes constitute only a very few of the many enzymes present in the organism, they have been studied in especial detail because they are produced in relatively large quantities and poured into the gut from which they can easily be obtained. They are divisible into three main types, according to the nature of the substances they digest. There are proteoclastic enzymes which break down proteins into their constituent amino acids (a series of different enzymes is necessary for the complete process), sucroclastic enzymes which convert the more complex carbohydrates or sugars, such as starch or cane sugar, into the simpler glucose, and lipoclastic enzymes or lipases which split up fats into the fatty acids and glycerine of which they are composed. These various end products of digestion are all capable of being absorbed by the cells lining the intestine, the insoluble fatty acids after emulsification, or their splitting up by physical processes into fine droplets, and the others in solution. The process of absorption, unlike that of diffusion whereby the inorganic salts pass through the walls of the gut, demands energy, work is done and oxygen accordingly utilized.

In the human digestive system the first enzyme is ptyalin secreted by one of the salivary glands and which converts starch into the simpler sugar maltose. In the stomach there is pepsin and also hydrochloric acid, and here protein digestion begins. The pancreas pours into the duodenum a fluid which contains enzymes capable of converting maltose and lactose

(milk sugar) into glucose, also lipase and a substance which when it comes in contact with another produced by the walls of the intestine produces trypsin which assists in the completion of protein digestion. The emulsification of fats is brought about by the bile produced by the liver. The secretion of the liver also contains the brown pigments responsible for the colour of the faeces. The acidity of the juices coming from the stomach is neutralized and the fluid in the intestine maintained at the right degree of alkalinity for the action of trypsin by the presence in the various secretions of sodium bicarbonate.

Digestion in man and in most of the more highly organized animals is extracellular, that is it takes place outside the actual cells and tissues, in the cavity of the gut. In simpler animals this is not always so. In protozoa where cells and tissues are absent and a gut impossible (although there may be a definite cell mouth) food is taken directly into the cytoplasm. Fluid which contains digestive enzymes elaborated within the protoplasm accumulates round the food and in this way small cavities or vacuoles are formed in which digestion takes place. Digestion of this type is called intracellular because it is carried out within the cells. It also occurs in sponges which, as we have seen, are in some respects just aggregations of protozoa. A variety of other animals digest their food by a combination of these two methods. For instance in the sea anemones and their allies the initial stages of protein digestion take place in the gut and the fine particles and soluble matter so produced are ingested by

absorptive cells in which digestion is completed. Bivalve molluscs are the most highly organized animals to retain the simpler type of digestion to any great extent and this is certainly related to the finely divided nature of their food (sifted from the water by ciliary action) much of which can be directly ingested. The influence of food on digestion is also seen in the relation which exists between the character of the food and the presence or relative strengths of the different digestive enzymes. Thus animals which feed exclusively on plants which are always especially rich in starch and other carbohydrates have very powerful sucroclastic enzymes, whereas carnivores have especially powerful proteases for the digestion of flesh but have frequently little or even no power of digesting starch. Omnivores, such as man, have powerful enzymes of all types.

Before we discuss the disposal throughout the organism of the digested food and its eventual fate, the accumulation of oxygen, without which the food would be useless, must first be considered. This process is known as respiration which, however, also includes the removal of carbon dioxide which will be dealt with a little later. In the protozoa and in the simpler multicellular animals there are no organs of respiration, oxygen entering freely by diffusion through the cell-membrane or general body surface as the case may be. But in more complex animals which possess a thicker body wall often strengthened in various ways for rigidity, protection or insulation from the environment, the entrance of oxygen is confined to definite regions. These organs of respiration vary much less

than do those of feeding because oxygen varies so much less than does food. Oxygen may be available in solution in water or in the gaseous state in air. Broadly speaking the respiratory organs of animals which live in water are called gills and of those that live in air lungs. Thus fish and marine molluscs such as snails and squids have gills, while terrestrial vertebrates such as man, and land snails have lungs. Frog tadpoles which live in water have gills but when they change into frogs and come on to land they develop lungs for breathing air though they also respire to a considerable extent through their very soft, moist skin. The insects and spiders possess characteristic respiratory organs called trachea, fine branching tubes which ramify through the body and open to the exterior usually at the sides of the body by pores called stigmata.

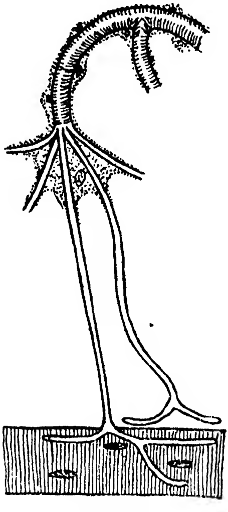


Fig. 4.

The terminal branches of the trachea in insects, showing the manner in which oxygen is carried directly to the tissues, muscles in this case (after Wigglesworth).

Gills are formed of very thin tissue through which oxygen can diffuse easily and rapidly and are usually much branched so as to expose the maximum possible surface for respiration. They are sometimes exposed, as in the common lugworm of our shores, but because of their

delicacy and great importance to the animal are more often sheltered in a cavity, as in the lobsters and crabs or in the marine snails and the squids, or protected by over-lapping flaps of skin as they are in fish. Special mechanisms ensure that a constant stream of water laden with oxygen flows over them. As fish swim water enters through the mouth and passes out through the gill openings on either side of the gullet just behind the mouth cavity, each opening being

Fig. 5.

Gills of the lugworm, *Arenicola*. Alternate branches have been removed (after Ashworth).

lined with delicate lamellated respiratory tissue. In certain fish, such as the mackerel, the demand for oxygen is so great that to obtain the necessary amount the animal has to keep continually moving. It becomes asphyxiated through lack of oxygen if it stops. In lobsters and crabs and their allies a small, continually moving appendage often called the baler causes a constant stream of water to flow over the numerous gills which develop as outgrowths from the base of the walking legs on either side of the body.

The lungs of vertebrates consist of a pair of elastic bags which lie suspended into the cavity of the thorax

(or chest). They develop as outgrowths from the under, or ventral, side of the digestive tube to the anterior end of which they are attached by the wind pipe or trachea. This is a single tube which opens at one end into the gullet at the glottis, and at the other end divides into two tubes called bronchi which communicate with the cavity of the lungs. Just below the glottis is the larynx. This is the organ of sound

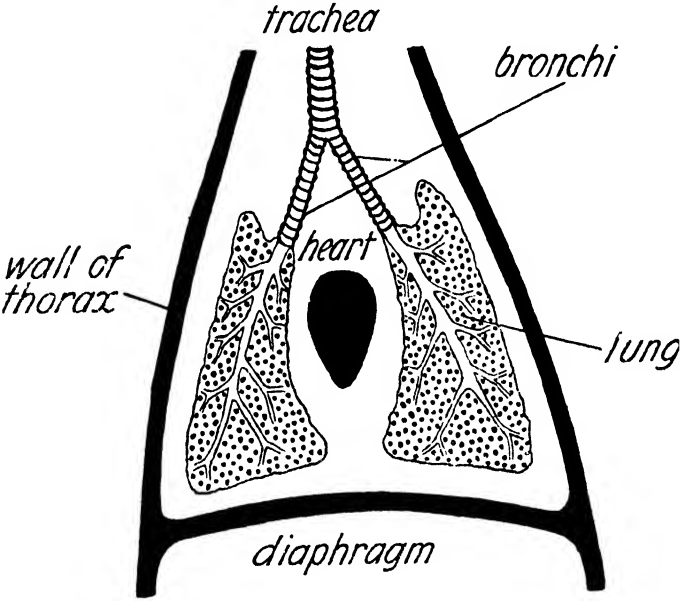


Fig. 6.

Diagram to show the structure and relations of the organs of respiration in mammals. The bronchi divide up within the lung into fine bronchioli which terminate in alveoli which are indicated by dots.

production and consists of a cartilaginous box containing the vocal chords. It is especially well developed in mammals. It is absent in the birds where sound is produced by a similar organ called the syrinx situated lower down about the bifurcation of the wind pipe.

The lungs are composed of spongy, respiratory tissue. They are comparatively simple structures in amphibians such as the frog (the most lowly type of land vertebrates), but in the higher vertebrates the greater need for oxygen is met by a greater complexity of the lungs, with a resultant increase in the respiratory surface. In man, and in the mammals generally, the bronchi divide repeatedly within the lung, the fine end tubes, or bronchioli, terminating in minute cavities called alveoli. It is in these that respiratory exchange takes place. There are some seven hundred million of these in our lungs and the respiratory surface so provided is some thirty times the surface of our bodies. The lungs of birds, the exceptionally high metabolism of which demands a correspondingly large quantity of oxygen, are even more complex than those of mammals. When air is drawn in it passes through the cavity of the lungs into a series of air-sacs, and returns through the lungs when expired. As a result birds respire not only when air is drawn in but also when it is expelled, unlike mammals and other vertebrates which respire only on the instroke.

The efficiency of the mechanisms for ensuring a flow of air over the respiratory surface in the lungs varies according to the oxygen needs of the animals. In frogs and other adult amphibians, air is

swallowed, that is pumped into the lungs by muscular movements in the mouth cavity. In the reptiles the cavity of the thorax is increased by an outward movement of the ribs and this causes air to be sucked into the lungs. When at rest birds respire by a similar mechanism but when in flight the actions of the great breast muscles which move the wings prevents this and air apparently enters through the nose and is later expelled by contractions of the abdominal muscles. In mammals the action of the ribs is assisted by downward movements of the diaphragm (see Fig. 6), a muscular partition (spasmodic movements of which cause hiccups) which separates the thoracic from the abdominal cavity. Opposite movements by ribs and diaphragm reduce the size of the thoracic cavity and force air out of the lungs.

The rate of breathing, and so of the amount of oxygen which enters the lungs over any period, is controlled by the needs of the animal. When we run or do heavy manual labour we breathe more and more rapidly. Regulation is carried out by the respiratory centre in the brain from which nerves carry messages to the muscles which control breathing. The respiratory centre is stimulated when there is an excess of carbon dioxide in the blood, that is when the end-products of oxidation are unduly plentiful, and it responds by causing an increase in the speed of the respiratory movements. Simple lack of oxygen, somewhat surprisingly, has no such effect. To this is due the mountain sickness which afflicts man at high altitudes. The rarified air contains comparatively

little oxygen yet the rate of breathing is not increased owing to the lack of any mechanism to produce this. The most obvious effect of the resultant lack of oxygen in the tissues is sickness.

2 Transport and Utilization of Energy

The way in which food is obtained and digested and oxygen secured by living organisms leads to the consideration of the manner in which these are transported from the gut and the respiratory organs to the various tissues, and of how they are eventually utilized. In the more simply constructed multicellular animals, even where a gut is present as in sea anemones and flatworms, oxygen and the products of digestion diffuse through the body or may, in the case of food, be carried in cells which are able to wander through the tissues. But in more complex animals some more elaborate mechanism is essential. Because of its motility, liquid is the ideal medium for this purpose and it is the body fluids of animals which constitute the means of transport.

These fluids consist of coelomic fluid, which invariably occupies the coelom or body cavity, and the more specialized blood. The former may be the only means of transport as it is, for example, in starfish and sea urchins, or it may work in conjunction with a partially developed blood system as in many worms. It is kept in movement either by the beating of cilia which line the body cavity, as in the starfish, or by muscular contractions of the body wall which occurs in worms.

Blood is by far the more important medium of transport. It is confined to definite vessels which ramify through the body and through which it is continually circulating. The more highly organized the animal and the greater its consequent need for energy, the more elaborate and efficient is this circulatory system. A brief description of it is a necessary introduction to that of the nature and properties of blood. In its fullest development the circulatory system has four main constituents: the heart, or pumping organ, the arteries which are thick-walled and elastic and in which blood is carried from the heart to all parts of the body; the capillaries which are exceedingly small and which ramify through the tissues; and finally the veins which are thin-walled and which carry the blood back from the capillaries to the heart.

The simplest type of circulatory system is found in the worms. It consists typically of two longitudinal

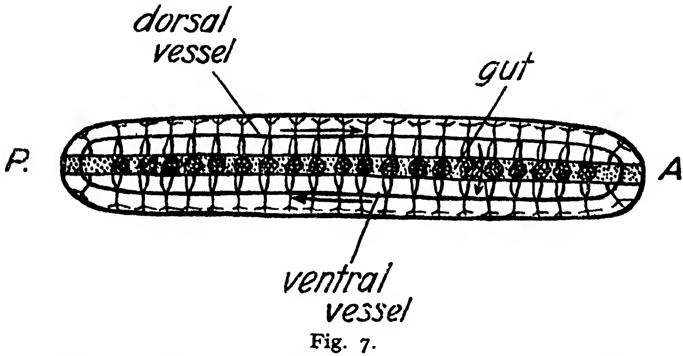


Fig. 7.

Diagram showing the arrangement of the circulatory system in the simplest annelid worms. *A*, anterior end; *P*, posterior end.

vessels, one above the gut, the dorsal vessel, and one below it, the ventral vessel. From these branches which terminate in capillaries pass to the body wall, and especially to the gills, if these are present, where oxygen is obtained, and around the walls of the gut where the products of digestion are collected. Circulation is usually maintained by muscular contractions, akin to the peristaltic movements of the gut, of the dorsal vessel, blood being continually passed forward along this and into the branches. In some worms certain of the vessels which pass round the gut are enlarged and very contractile and are known as hearts.

Animals higher in the scale of organization all possess a heart in which alone, with a few rare exceptions, the pumping action is localized. In crustaceans this is an elongated organ lying just below the superficial tissues on the upper side of the body and within a cavity called the pericardium. Blood collects in this cavity and is drawn into the heart when this expands through small pores or ostia along its

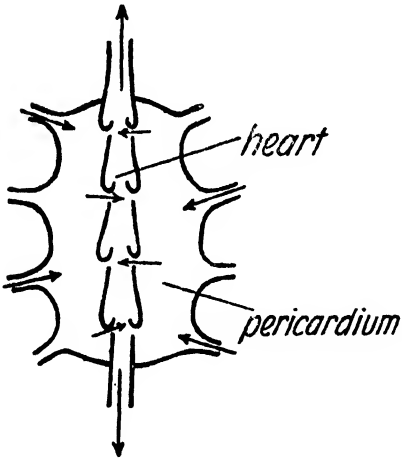


Fig. 8.
Diagram showing the structure of the heart in crustaceans.

sides. The succeeding contraction closes these openings and forces the blood both forward and backward into arteries at each end of the heart. Blood circulates through the tissues not by way of capillaries but in large spaces called haemocoels and then passes through the gills where respiration occurs before being drawn back into the pericardium. The circulatory system of insects appears at first sight surprisingly simple for animals which are only surpassed by birds in the muscular activity they display. But it will be remembered that their respiratory organs consist of trachea which carry oxygen directly to all parts of the body. It follows that the blood is concerned only with transporting the products of digestion (and with the later removal of the end products of protein metabolism), a task which demands much less complexity in the circulatory system than does the carriage of oxygen.

The conditions in the molluscs are not very different from those in the crustacea. Here also the blood passes from the heart through the arteries into blood spaces which surround the tissues and then through the gills back to the heart. Small branchial hearts are present in some of these animals and assist in the forcing of blood through the gills. The heart for the first time can be divided into distinct chambers; thin-walled auricles (of which there are usually two but may be four or only one) the dilations of which cause blood to be drawn in from the venous sinuses, and a single thick-walled ventricle which receives blood from the auricles and then, by powerful contractions, drives this by way of the arteries through the

body. Valves prevent the blood from flowing back from the auricles into the sinuses or from the ventricles into the auricles when these chambers contract.

The circulatory system is most highly developed in the vertebrates, and in all its members, fish, amphibians, reptiles, birds, mammals, it is constructed on the same ground plan, although the passage from fish which respire with gills to terrestrial vertebrates which respire with lungs entails corresponding changes

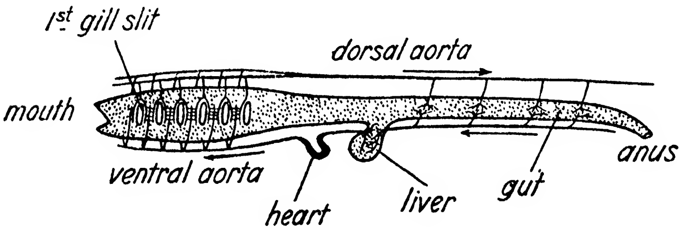


Fig. 9.

Diagram illustrating the circulatory system in a primitive, aquatic vertebrate. In air-breathing vertebrates it is essentially the same except that the capillary system in the aortic arches is lost and the complete set of six arches only occurs in the embryo (modified after Graham Kerr).

in the mechanism of circulation. The heart in fish lies on the under side of the body and is composed of four parts, a sinus venosus, thin-walled and non-contractile which receives blood from the veins, a single, thin-walled but contractile auricle, a very thick-walled and very powerful ventricle, and a tubular conus arteriosus, muscular and contractile, which merges into the first artery, the ventral aorta. From

either side of this artery a parallel series of arteries called aortic arches, usually five in number, pass round the sides of the body between the gill openings and reunite above to form the dorsal aorta. In their course are inserted capillaries which ramify through the gill tissue and enable respiratory exchange to take place. The dorsal aorta extends forwards and backwards and from it spring arteries which carry blood to all parts of the body. The capillaries in which these terminate (there are no haemocoels in the vertebrates) unite to form veins in which all the blood is eventually carried back to the sinus venosus and circulation is completed.

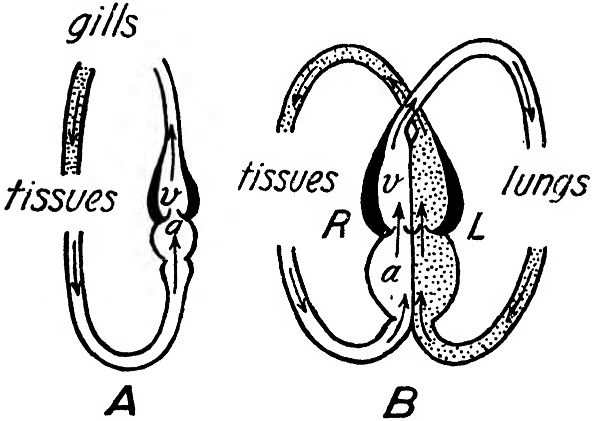


Fig. 10.

Diagram showing the differences between the single (*A*) and double (*B*) circulations typical of vertebrates possessing gills and lungs respectively. *a*, auricle; *L*, left; *R*, right; *v*, ventricle; blood containing oxygen indicated by stipling (modified after Graham Kerr).

In accordance with its greater need for oxygen the circulatory system of the very active fish represents a considerable advance in efficiency over that of the great majority of molluscs. The blood passes through the gills immediately after leaving the heart and while still at full pressure. Valves between the auricle and the ventricle and in the conus arteriosus prevent regurgitation. Unlike the primitive tubular heart where a continuous wave of contraction passes from end to end, in the fish the different chambers contract independently but in sequence. The capillaries and well-defined venous system are much more efficient than the haemocoels of crustacea and molluscs. One point about the venous system must be emphasized. All the blood from the intestine, which is laden with the products of digestion, passes by veins into the liver, the largest organ in the body, and is re-collected in a large hepatic vein which carries it to the heart. This hepatic portal system is present in all vertebrates and its significance will be shown a little later.

In the terrestrial vertebrates where lungs take the place of gills as the organs of respiration the circulation is modified. The original single circulation, heart→gills→body→heart, now becomes a double circulation for the blood after passing through the lungs returns again to the heart before being pumped through the body. There are thus two circulations, a pulmonary and a systemic, and the blood now follows the course, heart→lungs→heart→body→heart. The probable explanation for this lies in the inability of the heart to pump the very great amount of blood present in the

bodies of all terrestrial vertebrates, through the capillaries in both lungs and body in one operation. This double circulation involves a division of the heart which also loses the sinus venosus and the conus arteriosus. The division of the heart is only partial in the amphibians and the reptiles, the auricle but not the ventricle being completely divided, but in birds and mammals there are two ventricles as well as two auricles entirely separated from each other. Venous (deoxygenated) blood enters the right auricle and passes to the right ventricle from which it is pumped, by way of the pulmonary arteries to the lungs. It returns from these in the pulmonary veins (although no longer venous blood) which open into the left auricle, and from the left ventricle, which is much more muscular than the right ventricle, it is pumped on its long journey through the body. The right side of the heart is thus concerned with deoxygenated blood and the left side with oxygenated blood. In the amphibians and reptiles where the ventricle is only partially divided the blood in it is mixed and so the tissues do not receive exclusively oxygenated blood. This circulatory system is actually only a modification of that found in fish. Three of the aortic arches of fish are represented one by the carotid arteries which carry blood to the head, another by the pulmonary arteries and a third by the aorta (present on the one side only in birds and mammals) which carries blood from the left ventricle to the body, while the others, though absent in the adult, are present in the developing embryo. Living matter adapts old structures to meet new needs; in

the fish are present all the essential structures needed for the development of mammals.

Blood is continually being forced into the arteries from the heart. In a resting man the heart beats about seventy times a minute and delivers some fourteen pints of blood in this period. The increased demand for oxygen (and increased need for the disposal of waste products) caused by violent exercise may cause these figures to be trebled, the heart being stimulated by appropriate nerves. The valves of the heart are mechanically so perfect that they normally prevent regurgitation even under such conditions. Defects in these valves are one of the principal causes of heart trouble. Although the heart beats rhythmically, each beat causing a pulse in the arteries, blood is maintained at a fairly constant pressure owing to the elasticity of the arteries which are in a continual state of tension and so continue to squeeze blood through them between the contractions of the heart. This is very necessary because the capillaries are so extremely narrow that the friction of their walls slows down the rate of flow to about one thousandth of that in the aorta. An easy interchange of gases (oxygen and carbon dioxide), nutrient matter and the waste products of metabolism takes place through the delicate walls of the innumerable capillaries. Indeed some of the fluid from the blood oozes through these walls and circulates through the fine interspaces amongst the tissues. This lymph forms the fluid medium in which the cells live. It is collected in vessels known as lymphatics and pumped back into the veins by so-called lymph hearts.

The need for blood by the varouis tissues and organs varies from time to time. During mental activity the brain needs more blood; after a meal great quantities of blood collect round the intestine (we all know how difficult it is to do mental work at such times); during violent exercise blood is sent in unusually large amounts to the particular muscles involved. This distribution of blood is regulated by the arteries the muscular walls of which are under nervous control and can be dilated or constricted according to the needs of the organs they serve. A hormone called adrenalin (see page 96) also causes dilatation of the blood vessels.

The veins are simpler than the arteries and, as they contain blood which has passed through the capillaries since it left the arteries, they have no pulse. Blood flows through them at a steady pace and any tendency for it to flow back is effectively prevented by numerous small valves which permit blood to pass in the direction of the heart but not in the reverse direction.

It is now necessary to consider the nature of the transporting media, coelomic fluid and its more specialized derivative blood. These always contain soluble proteins and also inorganic salts which, in the more primitive marine animals, such as sea urchins, are practically identical in nature and concentration with those of sea water with which the body fluids of such animals are in equilibrium. In the course of evolution many groups of animals have emancipated themselves from such dependence on the medium in which they live; it is indeed one of the conditions which must be fulfilled before any animals can leave sea water. Thus

it comes about that the body fluids of freshwater animals contain a much higher, and essentially different, concentration of salts than that of the surrounding water, while, on the other hand, in the blood of many marine fish the salt concentration is lower than that of the sea water. Nevertheless even in terrestrial animals, such as mammals, the ancestors of which left the sea in remote ages, these same salts are present in much the same proportions as in sea water though in lower concentration. One explanation is that this represents the concentration of salts in the early oceans in which the early ancestors of the mammals lived, and with which their body fluids were in equilibrium. But in point of fact it is the very salts present in sea water which are essential for the maintenance of living matter, or this could never have originated, as it must have done, in the sea. And whenever animals have left the sea, or rather established that preliminary emancipation from its salt concentration, they had to retain within their body fluids those salts necessary for maintenance of living matter and in their correct proportions.

Two absolutely essential conditions must be fulfilled. There must be a proper *balance* between the antagonistic monovalent and divalent metallic ions, notably sodium and potassium and calcium and magnesium respectively, in the absence of which the cell-membranes on which the maintenance and properties of living matter are dependent, cannot be established. Then there must also be an adequate amount of the 'buffer' salts, such as the bicarbonates already alluded to, which ensure that the concentration of

hydrogen ions shall remain within the narrow limits within which alone can living matter normally exist.

Wandering cells occur in all coelomic fluids. They assist in the transport of food but are chiefly concerned with scavenging. They collect, by a process of ingestion or phagocytosis (they are frequently called phagocytes) akin to that of feeding in *Amoeba*, foreign matter, bacteria and waste particles, and convey these to the exterior. In some few cases there may be other cells containing one of the respiratory pigments described below.

Blood, like coelomic fluid, can be divided into a fluid 'plasma' and contained cells or 'corpuscles', the latter being characteristically very abundant. In the blood of all vertebrates these are divisible into white and red corpuscles. The former, which are usually the only type present in the blood of lower animals, are of several types (six have been identified in man).

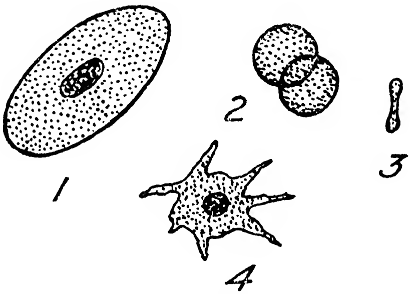


Fig. 11.

Constituents of vertebrate blood. 1, red blood corpuscle of amphibian, nucleated ; 2, red blood corpuscles of mammals, rounded, without nuclei and, as shown in (3), biconvex; 4, white corpuscle or phagocyte.

They wander through the tissues and their most important function is that, already described, of phagocytosis, but they may aid in the transport of food and, especially in the crustaceans, be concerned with the clotting of blood in the absence of which wounds would always be fatal. This process in the vertebrates is controlled by the non-cellular 'blood platelets' which cause precipitation of the insoluble protein, fibrin, from its soluble precursor, fibrinogen.

The red corpuscles of vertebrates are some five hundred times more numerous than the white and contain the pigment, haemoglobin. This is one of the respiratory pigments. These are proteins with an associated metallic element and they are able to combine loosely with oxygen, parting with it with equal readiness. When blood passes through our lungs the haemoglobin in the red corpuscles combines with the oxygen present in high concentrations in the alveoli and the unstable compound, oxyhaemoglobin, is formed. Later when the blood comes into intimate contact with the tissues as it passes through the capillaries it enters areas where the oxygen content is as low as it was high in the lungs. Under these conditions oxygen is released and passes into the tissues, it is 'unloaded' by the oxyhaemoglobin which is reconverted into haemoglobin; at the same time the bright red colour of the former is changed into a dull reddish purple, colours characteristic of arterial and venous blood respectively. This is the manner in which oxygen is carried from the organs of respiration to the tissues. A certain quantity is carried in solution in the plasma (which is the only

vehicle in some of the lower animals) but the fact that the presence of haemoglobin in our blood enables it to carry forty times as much oxygen as it otherwise could reveals how inadequate for the needs of a vertebrate is this primitive method.

Haemoglobin occurs in all vertebrates and also appears sporadically amongst the worms, insects and molluscs. But in these animals it is usually in solution in the plasma and not in corpuscles which, because of the immense surface they expose for oxygen exchange, are the more efficient vehicle. The metal associated with haemoglobin is iron, which is also present in another respiratory pigment, haemerythrin, found in the corpuscles of body fluids in certain worms. A much more important pigment than this last is haemocyanin which occurs in the majority of molluscs and crustaceans. It contains copper and is blue when oxygenated and becomes colourless when it loses oxygen. It is always carried in solution in the plasma and, although adequate for the needs of the animals which possess it, is much less efficient than haemoglobin. A respiratory pigment called cytochrome has recently been identified in all types of living matter, plants and bacteria as well as animals, it is of vital importance in respiratory processes within the cell and like haemoglobin which is probably derived from it, contains iron.

As its simplicity in insects, where oxygen is carried direct to the tissues in the trachea, indicates, the extreme elaboration of the circulatory system is concerned with the transport of oxygen (and removal of carbon dioxide) rather than with that of nutriment.

Of these, glucose and amino acids, like the salts, are carried in solution and fats in suspension as fine droplets. They are needed for maintenance of the tissues, making good the continual breakdown due to metabolism, for growth and for the elaboration of the sexual products. It is the amino acids, out of which proteins are built up, that are especially needed for these purposes. Proteins with carbohydrates and fats form the fuel which, in the presence of oxygen, is burnt to produce energy, fat being, weight for weight, rather more than twice as efficient as either of the others. Glucose can be converted into fats (which is the reason why stout people are forbidden starchy foods) and so fat is not, as are proteins and carbohydrates, an absolutely essential constituent of food.

The bare maintenance of life demands a constant supply of energy. This is known as basal metabolism. Work of any kind, even the transmission of a nervous impulse, increases this minimal demand. Feeding and digestion are usually intermittent but the call for energy is incessant. Large reserves of carbohydrates and fat are accumulated to answer this. In the vertebrates fat is stored amongst the tissues generally and especially just beneath the skin, but glucose is intercepted by the liver into which it is carried by the hepatic portal system immediately after absorption. In the liver it is changed into a more complex carbohydrate called glycogen, or animal starch, which is insoluble. This storage of carbohydrate is one of the chief functions of the liver. Glycogen is constantly being reconverted into soluble glucose and passes into the blood stream

which normally contains about 0.1 per cent of it. In the disease called diabetes, owing to the absence of the hormone insulin (see p. 95), the tissues are unable to utilize glucose and the liver to retain it in the form of glycogen. As a result the sugar content in the blood quickly rises to an abnormal and dangerous extent.

Mammals and birds need especially large quantities of food from which energy can be obtained because, unlike all other animals, they maintain a constant, high body temperature. They are the so-called 'warm-blooded' animals in contradistinction to the 'cold-blooded' in which the temperature of the body varies with that of the surroundings. Our own body temperature remains remarkably constant around 98.4 degrees F., that of birds is much higher, averaging about 106 degrees F. Only sometimes in the tropics and less frequently during the summer in the temperate regions when the air temperature rises very high have warm-blooded animals the same temperature as their surroundings. Elsewhere they must liberate energy in the form of heat, either by the direct oxidization of food or as a bye-product of muscular activity. The heat produced in our bodies by muscular activity is obvious while the spasms of shivering which seize us when we are chilled have as their object the production of heat. It is essential that heat should be retained as far as possible, if it is dissipated too rapidly the strain on the metabolism becomes too great, and both the hair of mammals and the feathers of birds are non-conducting layers which reduce the loss of heat by radiation. The absence of a complete hairy covering in man is

probably connected with his adoption of artificial coverings, first the skins of animals and later woven cloth. Loss of heat is also prevented by the accumulation of fat under the skin, and this is of very great thickness in marine mammals where hair is useless for insulation. The blubber of whales provides the supreme example. Should the body temperature tend to rise too high, as a result of strenuous exercise or great heat from the sun, heat is dissipated in various ways, by radiation from the surface of the body, by evaporation of water from the lungs and, in many mammals, by the evaporation of perspiration produced by special glands in the skin.

The bulk of the salts which diffuse through the walls of the gut are used for the maintenance of the salt concentration in the blood. Certain elements are needed for specific purposes, for instance iron is needed for the formation of haemoglobin, copper for haemocyanin, calcium for bone, and iodine for the elaboration of the secretion of the thyroid (see p. 95). The vitamins or accessory food substances form an inconspicuous but absolutely essential constituent of the food. In mammals, where alone they have been investigated, eight vitamins have so far been isolated, known as vitamins A, B1, B2, B3, B4, C, D and E. Exactly how these substances influence metabolism is unknown but their absence is invariably accompanied by various deficiency diseases, such as scurvy, beri-beri, and rickets, by stoppage of growth or by sterility.[1]

[1] A good general account of vitamins is given in the volume on chemistry in this series.

The production of energy by oxidization in the tissues results in the formation of substances which have to be removed as quickly as possible. Both carbohydrates and fats are converted into carbon dioxide and water. This is the eventual fate of the bulk of the amino acid molecules, but first of all the nitrogen in them is removed with the formation of ammonia (NH_3). This process takes place largely in the liver where the ammonia, which is somewhat poisonous causing convulsions if too plentiful in the blood, is combined with appropriate quantities of that other waste product, carbon dioxide, to form the very soluble and innocuous compound urea ($CO(NH_2)_2$). Other soluble nitrogenous compounds formed by the break-down of proteins in the tissues include the more complex uric acid, which is much more abundant than urea in most animals though not in mammals, and creatinine, while the sulphur and phosphorus present in some proteins is finally passed back into the blood stream largely in the form of sulphuric and phosphoric acids.

The blood transports food and oxygen to the tissues, it also carries away the end products of metabolism into which they are finally converted. It remains to be seen how these are removed from the body. This is known as excretion and it must be carried out as quickly as possible for the accumulation of these waste products first impedes metabolism and finally poisons the entire system.

The more complex the organism and the greater its consequent need for energy, the more elaborate and efficient, as we have seen, are the means of obtaining

and distributing food and oxygen, and the more efficient also must be the mechanism of excretion. Carbon dioxide is excreted primarily by the organs of respiration, gills or lungs, which are concerned equally with the taking in of oxygen and the removal of carbon dioxide, in short with all gaseous exchange. The manner in which excess of carbon dioxide causes increased respiratory movements has already been described. Water is also removed in this way (the air we expel from our lungs is always laden with water vapour) as well as through the skin and by the true excretory organs.

These organs are found in the simplest state in flatworms. Simpler animals, such as sea anemones, do not possess them, waste matter either diffusing out or being carried to the exterior by wandering cells. Exceedingly fine tubes opening to the exterior have at their blind inner ends cells which can extract waste matter from the coelomic fluid. Long, vibratile processes project into the tube from these cells and by their movement, the resemblance of which to the flickering of a flame has given rise to the name 'flame cell', drive the excretory fluid to the exterior. In creatures such as the earthworm the excretory organs are called nephridia and a pair of these is present in the great majority of the segments into which their bodies,

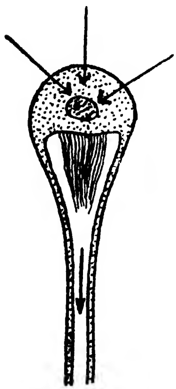


Fig. 12.
Flame cell of a flatworm.

and those of similar worms, are divided. Each nephridium consists of a long coiled tube opening to the exterior at the side of the body and with a funnel at the other end which opens into the body cavity. This funnel is covered with cilia the beating of which drives particles of waste matter down the tube and so out of the animal. A section of the tube which is surrounded by capillaries is able, like the flame cells, to extract nitrogenous and other soluble excretory matter from the blood and this also is passed out. In crustaceans and molluscs where the great development of the haemocoels causes the almost complete obliteration of the true body cavity, the excretory organs are usually confined to a single pair open to the interior only in the molluscs.

In the vertebrates the excretory organs, as we should expect, are much more complex although of essentially the same character. A large number of tubules, which open into the body cavity only in the

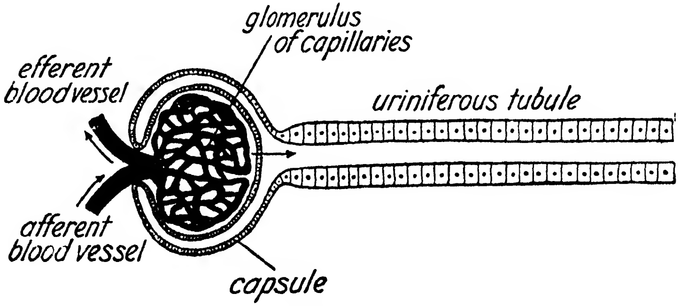


Fig. 13.

Diagram showing structure of a tubule in the human kidney.

most primitive vertebrates, are contained in a single compact organ called a kidney. Each of our own kidneys contains about one million tubules. The end of each tubule is expanded and infolded, the cavity so formed being occupied by a rounded mass of capillaries known as a glomerulus. The blood as it passes through these capillaries is apparently filtered, all its constituents passing through except the corpuscles and the dissolved proteins. The filtered fluid which passes down the tubules consists of water, with salts, glucose and urea. Of these the two former are largely reabsorbed by the cells lining the tubules and so returned to the blood while at the same time other waste matter, such as uric acid, more urea, creatinine and ammonia, are removed from the blood by these cells and added to the urine. This trickles down the tubules into the centre of the kidneys and so into the ureters which in turn open into the bladder. Here it accumulates and is expelled from time to time. A man under normal conditions produces some two and a half pints of urine daily.

In the vertebrates, and probably in all animals, the gut also plays some part in excretion, notably in the removal as in ourselves of matter which is only slightly soluble and might block the excretory tubules. In vertebrates these are passed into the rectum.

3 Reception and Response

Irritability, it will be recalled, is one of the fundamental properties of living matter. All organisms are able to perceive changes in the world around them and

to make suitable reactions. They possess the powers of reception and response. This is true of the simplest of animals, such as *Amoeba*, but there are no special organs for either purpose, the protoplasm itself both perceiving changes and making appropriate reactions. In the multicellular, and even in the more complex non-cellular, animals definite organs are always present. The receptor organs, commonly but less accurately designated sense organs, receive impressions from the external and the internal environment. All our knowledge of the world we live in comes to us through these doors into our consciousness and is bounded by their limitations. Response to the stimuli received by the receptors is made by the various effector organs, such as the muscles, which, in the adult animal, utilize most of the energy obtained by feeding and respiration. The receptor and effector organs, which may be widely separated, are linked together usually by nerves but also by other transmitting and co-ordinating mechanisms. These will be considered in the next chapter, attention being confined here to the chief receptor and effector organs.

In their simplest form these two types of organs may be united within the same cell, the intervening link being absent. In the hydroids, the simplest allies of the sea anemones, there are so-called myoepithelial cells with a narrow, outer portion in contact with the surrounding water and a broad, inner portion capable of contracting. The first portion of the cell receives impressions, is a receptor, the second responds to these by appropriate contractions and so is an effector. In

the somewhat more complex sea anemones there are separate receptor cells on the outer surface of the body and well-developed muscles deeper in the tissues with an intervening nervous system. This is true of all higher animals.

Receptors may be divided into those concerned with external and those concerned with internal stimuli, known respectively as exteroceptive and proprioceptive organs. The former are further divisible into those affected by contact stimuli (organs of touch), chemical stimuli (including the organs of taste and smell),

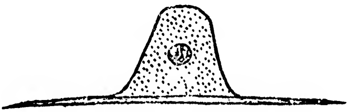


Fig. 14.

Myoepithelial cell from the superficial tissues of a hydroid, the upper portion receives stimuli, the elongated lower portion responds to these by contracting.

gravity (organs of orientation), sound waves (organs of hearing) and light waves (organs of vision).

Though always important, the sense of touch may be of primary significance in animals where neither sight nor smell is well developed. The organs of touch are very simple, often consisting merely of free nerve endings in the skin and at their most complex of no more than small corpuscles formed by a group of cells. They are particularly abundant in certain organs which are in frequent contact with the surroundings, such as the tentacles of sea anemones, the antennae of crustaceans and insects, or our own finger tips, while the long

whiskers of many mammals and the long nose of moles or shrews are associated with organs of touch. Although the precise property of the surroundings which influences the different tactile organs in other animals cannot be determined, simple experiments on our own bodies reveal that the numerous sense spots scattered over the skin have different functions, some being affected by contact pressure, others by warmth or by cold, and others again registering pain.

Only in air-breathing animals can the senses of taste and smell be distinguished. Both are concerned with chemical stimuli, in the former in solution, in the latter in gaseous form. Accordingly, though fish have olfactory organs akin to our own they must be concerned with substances in solution. Aquatic animals in general seem able to detect the presence of substances in solution. Thus the presence of food near them will cause sea anemones to expand and crustaceans to search actively for it. In sea urchins, starfish or in bivalve molluscs the discharge into the water of sexual products will induce members of the opposite sex to spawn. It is impossible, however, in such animals to distinguish the receptors affected by chemical stimuli from those concerned with touch.

In the insects and in the terrestrial vertebrates there are distinct organs of taste and smell. Certain insects certainly detect their food by its smell and also members of the opposite sex, while they possess organs of taste in the mouth parts or in the anterior regions of the gut. In the mammals the sense of smell located in the olfactory organ or the nose is usually

extraordinarily acute and often more important than that of sight. This is particularly true of ground living animals which detect their prey or their enemies in this way. The world of a dog has aptly been described as " mainly a world of smells " (Haldane and Huxley). In man this sense is largely vestigial, probably because he is descended from arboreal animals where sight is of more importance than smell. Nevertheless we are still capable of detecting substances in extremely low concentrations.

Taste in man and other vertebrates is confined to receptors in the tongue and other parts of the mouth cavity and anterior end of the gullet. These organs consist of groups of elongated sense cells enclosed in a sheath of ordinary cells and are known as taste buds. There are actually only four kinds of taste, sweet, sour, salt and bitter, and the impression of taste we receive is a combination of these together with impulses from the olfactory organ ; the apparent taste of a substance may be profoundly altered if the nasal passages are blocked, as in a cold, and the sense of smell no longer operative.

The influence of gravity on the majority of animals is profound though far from obvious. Men seldom even realize that they possess an organ of orientation unless it becomes diseased and they find themselves unable to stand upright. A knowledge of their position in relation to the earth is essential to all animals which move. Those which are fixed or have very limited powers of movement, such as barnacles or sea anemones, alone are devoid of organs of orientation. These are

essentially the same in all animals. In their simplest form they consist of a small spherical cavity called a statocyst lined with groups of sensory cells bearing long hairs and containing fluid and a solid, heavy body which is influenced by gravity. As the animal moves about this heavy statolith bears first against one set of

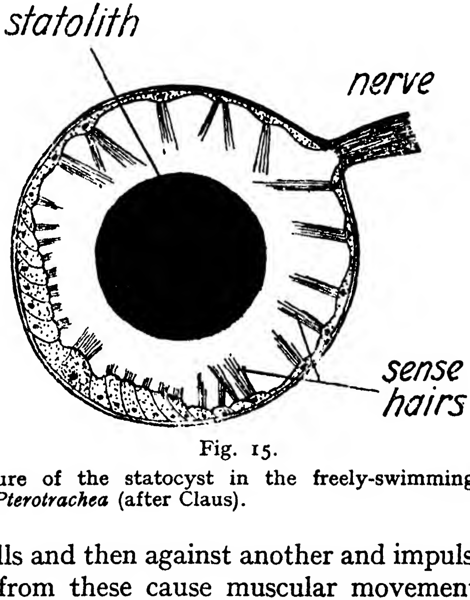


Fig. 15.

Structure of the statocyst in the freely-swimming univalve mollusc, *Pterotrachea* (after Claus).

sense cells and then against another and impulses transmitted from these cause muscular movements which right the animal. A very beautiful and much-quoted experiment proves this. In certain crustaceans the statolith consists of small sand grains which enter the cavity of the statolith when the animal moults. If these are replaced by iron filings the animal can be made

to swim upside down or at any angle by placing a magnet at suitable positions. Gravity is replaced by magnetic attraction and the animal orientates itself to the position of the magnet instead of to that of the earth.

In the vertebrates the organ of balance is more complicated, consisting of a large chamber, the utriculus, into which open three semicircular canals,

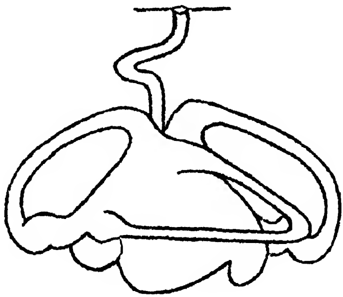


Fig. 16.

Left otocyst of a Dogfish (*Acanthias*) showing central utriculus, three semicircular canals each with an ampulla, or swelling, at one end, and above the endolymphatic duct leading to the exterior (after Graham Kerr).

two of which are vertical though at different angles and the third horizontal. Each possesses a swollen portion or ampulla at one end containing sensory cells with projecting hairs. In the utriculus are more sensory cells and a heavy calcareous body usually called an otolith. The whole organ is filled with fluid called endolymph. Movements in any direction cause corresponding changes in the position of the otolith and

movements of the fluid in the semicircular canals, different sensory cells are continually being stimulated and so appropriate muscular reactions induced which keep the animal correctly orientated.

Hearing, or the detection and analysis of sound waves, is confined essentially to terrestrial animals, although probably some aquatic animals can detect vibrations in the water too low in frequency to produce a continuous sound. This appears to the main function of the lateral-line sense organ in fishes which is certainly capable of detecting electric currents in the water and is enervated by what becomes the auditory nerve in higher vertebrates. Amongst invertebrates hearing is apparently confined to insects which have auditory organs in their limbs or in the abdomen consisting of a disc or tympanum which vibrates at different rates according to the composition of the sound and a sense organ for analysing these vibrations. In vertebrates the organ of hearing is associated with that of balance of which it is essentially an outgrowth, indicating that the statocyst of simpler animals may be affected by sound waves. This organ becomes more and more complex in the ascending series of the vertebrates being most highly developed in the mammals.

The human auditory organ consists of three parts. The outer ear consists of the lobe which collects sound and is much more efficient in, for, example, a dog than it is in ourselves. The middle ear is made up of the ear drum, which vibrates in the presence of sound waves, and of an internal cavity which is in communication with the back of the throat, pressure on both sides of

the ear drum being thereby equalized, and is bridged by three small bones known as the auditory ossicles. These convey vibrations from the ear drum to a small oval window, or fenestra ovalis, in the bony mass of the skull within which lies the inner ear. This consists, in addition to the organs of balance already described, of a

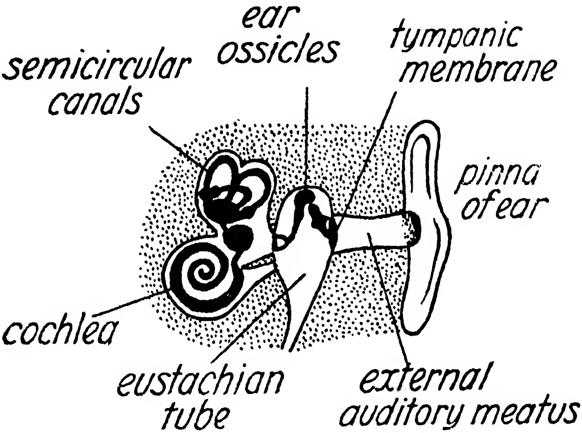


Fig. 17.
Diagram of a human ear.

projection from the utriculus called the sacculus which in turn leads into a spiral structure called the cochlea which is the actual auditory receptor. The structures of the inner ear are surrounded by a fluid called the perilymph and all vibrations transmitted by the ossicles from the ear drum to the fenestra ovalis pass through this fluid, a second window lower than the first, which moves with it, permitting of this. The

cochlea in man contains some ten thousand fibres, each of which probably vibrates to one note only, fine branches from the auditory nerve being connected with each and transmitting impulses to the brain. By this elaborate mechanism different sounds can be analysed into their components and the whole put together again, as it were, in the brain. Our organ of hearing is one of the most complex receptors and is capable of perceiving sound waves over a range of eleven octaves, of which seven are used in music. It is noteworthy that the capacity of producing sound goes hand in hand, in both vertebrates and insects, with the power of hearing.

Light has probably a greater effect on animals than any other external factor and light receptors are correspondingly widespread. These range from tiny spots of pigment present in certain protozoa and groups of one or more sense cells found in the simpler multicellular animals through organs of increasing complexity to the extremely elaborate eye of the vertebrates and the most highly organized molluscs such as the octopus and squid. Beginning with the mere perception of light these proceed probably by way of distinctions between different light intensities to an increasing perception of form, probably without distinctions between colours, and finally to clear image formation

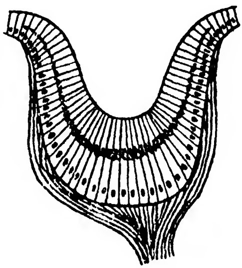


Fig. 18.

Eye of the limpet, *Patella*, an example of a simple eye consisting of retinal cells lying in an exposed pit each cell being connected with a nerve fibre.

and full colour vision. In multicellular animals the simplest type of light receptor occurs in the jellyfish and consists of a few sense cells surrounded by pigment and called an ocellus. This probably assists the statocysts in the orientation of the animal. The simple eye appears in many worms, in the more primitive molluscs and in spiders. It may possess a lens for focussing light on to the sensory cells or retina, stimuli so received being transmitted as impulses in optic nerves. Such eyes are certainly incapable of image formation. From this simple eye have developed the

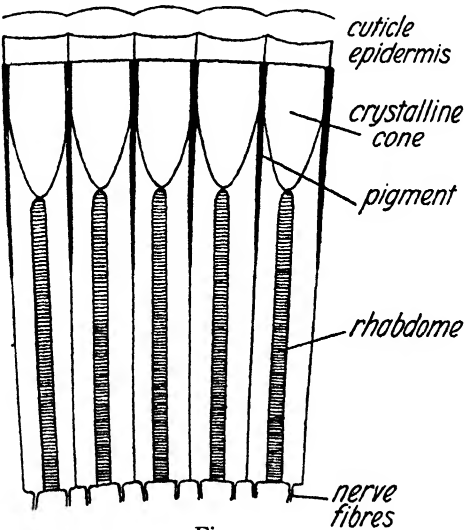


Fig. 19.

Diagram illustrating the structure of the mosaic eye characteristic of crustaceans and insects, five omatidia out of many alone being shown. Such eyes are capable of perceiving adjacent objects much more clearly than distant ones.

two more complex types, the mosaic and the camera eye, characteristic of the most highly organized animals, the former occurring in insects and crustaceans and the latter in the highest molluscs and in the vertebrates.

The mosaic eye actually consists of a great number of individual eyes or ' omatidia ' arranged in a compact round or oval mass. Each omatidium consists essentially of a superficial lens[1] which focuses light upon the deeper, sensory region, and is usually separated from its fellows by a layer of black pigment. In certain night flying insects this pigment may be absent while it can be withdrawn in various crustaceans, the result being a greater internal illumination. As far as can be determined a small portion of the field of vision is received by each of the omatidia, which may exceed two thousand in each eye of the common housefly, the complete picture being made up in the brain from the various ' pieces ' conveyed to it by the optic nerves. Insects seem capable of colour vision though possibly only to a limited extent.

The fully developed camera eye, characteristic of the vertebrates and the highest molluscs, is a spherical structure enclosed in a tough membranous case or sclerotic with a transparent window called the cornea in front. In its simplest form (in the mollusc, *Nautilus*) light enters through a tiny aperture, like that of a pin-hole camera. But in all the vertebrates and in the majority of molluscs with this type of eye the focusing mechanism consists of a transparent, glassy lens

[1] The crystalline cones probably reverse the image reversed in the first place by the lens.

attached to which are muscles which enable it to change in position (molluscs, bony fish, amphibia, reptiles and birds), or in shape (mammals), and so focus near or distant objects with equal distinctness on to the receptive retina. This is a purely physical process and defects in this portion of our eyes can be remedied by

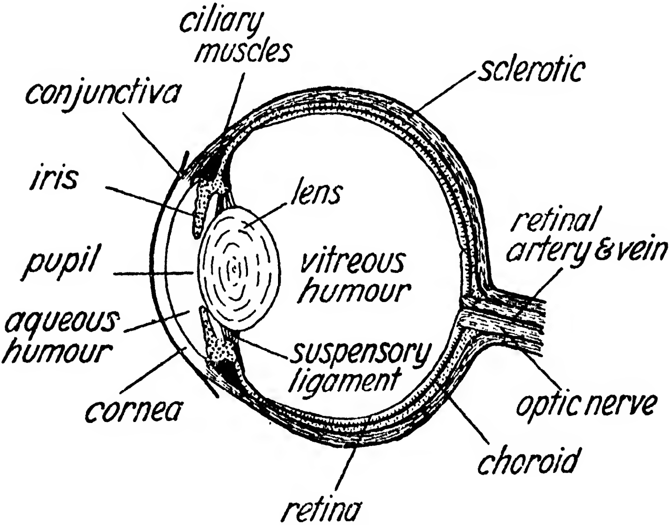


Fig. 20.
The vertebrate eye.

using spectacles with appropriate lenses. In front of the lens is an iris diaphragm, the movements of which control the amount of light which enters the eye. The central opening is called the pupil ; this enlarges greatly when we enter a dark room and is correspondingly reduced when we pass into bright sunshine.

The cavity of the eyeball is filled with transparent substances, the fluid aqueous humour between the cornea and the gelatinous vitreous humour between the lens and the retina. This receptor surface occupies the greater part of the internal surface of the eyeball. It consists of two elements known, because of their shape, as rods and cones, the former being possibly concerned with colour perception and the latter exclusively with light intensity and so being of particular use in dim light. In the vertebrates, though not in the octopus or squid, the eyes of which are in this respect more efficient than our own, the nerve fibres which connect with the retinal cells pass over their outer exposed surface so that light has to penetrate through them (and also through blood vessels) to reach the retina. The place where the optic nerve passes through the retina is called the blind spot, for here the receptor surface is interrupted. In between the retina and the sclerotic is a layer of cells called the choroid containing black pigment which prevents reflection of light.

Light is transmitted in the form of waves and our retina is stimulated by only a single octave of these, ranging in length from violet (0.0004 mm.) by way of indigo, blue, yellow, orange, to red (0.0008 mm.). A mixture of all these gives the sensation of white, as do mixtures of red and blue green, or of green and violet, the two constituents being known as complementary colours. Light of a single wave length gives the impression of a true colour or mixtures of light of neighbouring wave lengths give an intermediate colour, for example, yellow and blue give green. Our own eyes,

being situated at the front, and not at the sides of the head, as they are in the majority of animals, are capable of both focusing on the same object, the eyes being moved in their sockets by a group of six muscles found in all vertebrates. Estimation of perspective and judging of distances are largely, though not entirely, due to this power of binocular vision.

The proprioceptors concerned, it will be remembered, with internal changes are everywhere abundant in the body, in muscles, tendons and joints, in the walls of the gut and in the other deep tissues. They are allied to the tactile receptors and play an essential rôle in the co-ordination of movement and other essential functions. Any interference in the passage of impulses from them to the brain interferes seriously with the functioning of the organism as a whole.

Of the effector organs the most obvious are those concerned with movement. Three types of movement

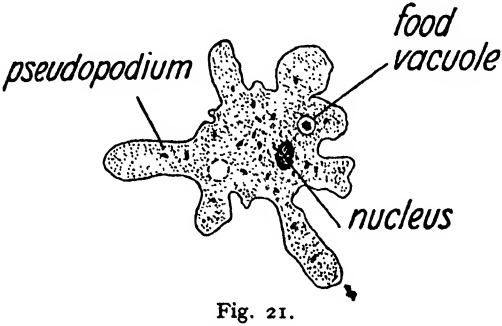


Fig. 21.

Structure of *Amoeba* showing formation of irregular pseudopodia, the organs of locomotion and food capture.

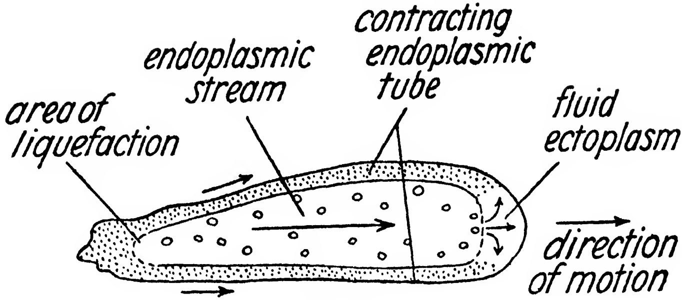


Fig. 22.

Diagrammatic representation of amoeboid movement, the relatively firm, outer ectoplasm is continually being converted into more fluid, inner endoplasm at the hind end and streaming forward, to be reconverted into ectoplasm, at first in a fluid state to permit of forward movement, at the front end (after Pantin).

occur in animals, amoeboid, muscular and ciliary. Amoeboid movement is the most fundamental type of motion and is found in the simplest protozoa, such as *Amoeba*, and in the wandering cells or leucocytes of the body fluids of higher animals. It consists of streaming movements of the protoplasm brought about, apparently, by continuous reversible changes in its physical properties (see Fig. 22).

Muscles are composed of cells which have the special power of altering their shape and so contracting when they are stimulated. In the vertebrates three types of muscle, different in their structure and properties, are distinguished. Striped muscle consists of long, multinucleated fibres with characteristic cross striations, the function of which is obscure, but may be the prevention of internal friction. These muscles are the prime

movers of the body, being attached to the skeleton by tough cords called tendons. The posture of the body is also maintained by these muscles which are in a constant state of partial tension or tonus. They are innervated by branches from the central nervous system (see next chapter) and contract only when stimulated, a single nerve impulse producing a quick single contraction, a series of impulses, some forty-five per second in man, being necessary to produce continued contraction or tetanus.

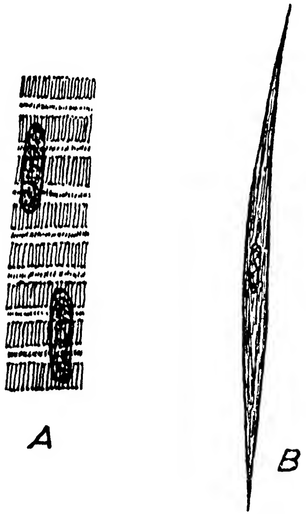


Fig. 23.
A, striped muscle; *B*, smooth muscle.

Smooth or visceral muscles have no striations and are uninucleated. They occur in the viscera, notably in the walls of the gut and arteries. They are supplied with two sets of muscles from the sympathetic nervous system (see next chapter), but they contract spontaneously, they are voluntary muscles unlike the involuntary skeletal muscles. Smooth muscle will continue to contract for some time after it has been removed from the body whereas excised skeletal muscle has to be excited by stimulating its attached nerves. The two

sets of nerves control the spontaneous contractions, one set augmenting and the other inhibiting them, responses to stimuli being slower and longer but less powerful than those of striped muscle. Finally, there are muscles intermediate between these two, notably the heart muscle, the whole organ in this case acting as a unit, stimulation of any portion affecting all other portions. In the invertebrates, apart from molluscs and the crustaceans, insects and spiders, these differences between the muscles, which are differences of degree rather than kind, do not occur, all the muscles of, for instance, a worm, being smooth.

Muscular contraction involves the breaking down of the organic compound phosphagen, the requisite energy being released thereby and also heat which can actually be measured. No oxygen is used in this process, but a recovery process follows in which phosphagen is reformed, the energy for this being usually obtained by the oxidation of available matter, usually carbohydrates. But even this process can proceed for some time without oxygen energy being then liberated by the conversion of glycogen into lactic acid.

In many animals, notably molluscs, crustaceans, insects, spiders and vertebrates, there is a hard skeleton to which the muscles are attached, though it also serves for support and often for protection. It is impossible here to describe these often highly complex structures but it should be noted that they may be external, as in crustaceans and insects, or internal, as in vertebrates. In the former the different portions, strengthened by calcareous or horny material, are united by thin,

flexible membranes which permit them to move in various planes. The internal skeleton of vertebrates consists of cartilage or bone, the various portions being accurately jointed together. It may be divided into various regions. The skull, or head skeleton, forms the jaws and the cranium which protects the all-important brain and major sense organs; it becomes stronger and more complete in the ascending scale from fish to mammals. The axial skeleton consists of the many-jointed backbone or vertebral column which encloses the spine and is the pre-eminant characteristic of the vertebrates. The appendicular skeleton consist of the fore and hind limbs with the girdles, shoulder and hip regions respectively, to which they are attached. There remain the ribs and the breastbone or sternum, which protect the chest and assist in respiratory movements, and the so-called visceral skeleton which in fishes forms the skeleton of the gills and in higher vertebrates that of the tongue and larynx.

Before leaving muscles an important effector organ found in a few fishes and which appears usually to be derived from them must be mentioned. This is the electric organ. In fish such as the Torpedo Ray of the Mediterranean and the Electric Eel, *Gymnotus*, of South American rivers, it is composed of modified muscles which form series of plates, exceeding one hundred thousand in the Torpedo Ray, insulated from one another by connective tissue and constituting a great accumulator of electricity which is discharged on nervous stimulation. In the Electric Catfish, *Malapterurus*, the organ is derived from the skin glands.

Broadly speaking these unique organs may be described as muscles or glands in which the electric current which is a by-product of normal activity has become the chief product. A current of about 450 volts is produced by *Malapterurus* and of some 30 volts by *Torpedo*, the electric organs thus constituting very efficient means of protection or attack.

The fine, vibratile hairs called cilia, which are borne on the free surface of cells, are widespread in the animal kingdom, they form the means of locomotion and of food collection in many protozoa and occur in various parts of the body, notably the mouth and trachea, in vertebrates. When examined under the microscope the beating of cilia resembles nothing so much as a field of corn blown by the wind. All the cilia on the same row beat simultaneously, being followed immediately afterwards by the preceding row and so on. The careful study of individual cilia reveals that the effective beat consists of a rapid forward stroke which produces a current in the adjacent fluid, on the completion of the forward stroke the cilia lose their rigidity, the recovery beat being slow and lax. The mechanism underlying ciliary action is very difficult to investigate because cilia are so small, but there is some evidence that it is

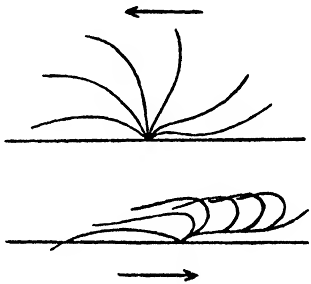


Fig. 24.

Ciliary movement; *above*, effective beat; *below*, recovery (after Gray).

akin to that of muscular action (and amoeboid movement).

The second great group of effectors are the glands. These are concerned with the process of secretion, that is the production from the blood of substances needed by the organism. They are very numerous. Amongst the most obvious examples in our own bodies are the sweat glands which produce the watery secretion the evaporation of which lowers our body temperature, and the salivary glands which assist in digestion and swallowing. The majority of glands open as do these either on the surface of the body or into the gut, but there are others, to be mentioned later, which pass their secretion back into the blood. These are the so-called ductless glands. Glands may be simple pockets or unbranched tubes, like our sweat glands, or be very large structures composed of many branching tubes like the liver. Their cells are characteristically large and contain, before discharge, granules of the substance they elaborate. During secretion the oxygen consumption of a gland may be doubled and, though the actual process is still very imperfectly understood, there seems little doubt that

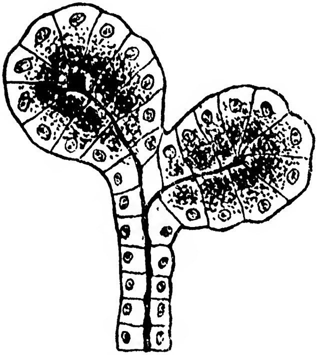
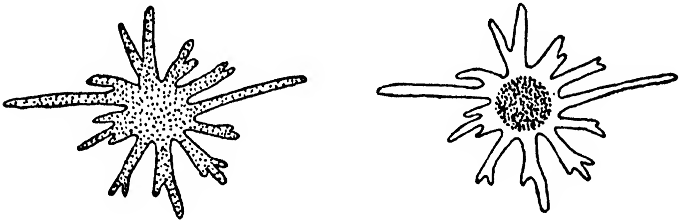


Fig. 25.
Portion of vertebrate pancreas showing secretion in cells, and ducts which carry this away.

secretion will eventually be explained along purely physical lines.

Two other effectors, neither of which occur in our own bodies, call for mention, namely those concerned with colour response and with light production which are allied respectively to the first and second groups of effector organs. Crustaceans, fish, amphibians and reptiles may possess pigment cells in the skin, the reactions of which enable their owners to change in



A B

Fig. 26.

Pigment cells, or melanophores, of fish. *A*, pigment expanded; *B*, pigment contracted.

colour and so frequently assume the colour or pattern of the background. The cells are branched but it is the movements of the pigment and not of the actual cell which is responsible for colour change. It is held by certain biologists that these cells are essentially the same as smooth muscles. Light production or luminescence occurs in very many marine animals from protozoa to fish and in certain insects such as the glow-worm and the fire-fly. It is produced in organs which may be simple glands which secrete a slimy, luminous

substance or may be very elaborate with a reflector behind and a lens for projecting the light in front. Light is produced by the oxidization of substances called luciferins with the aid of enzymes called luciferases. It

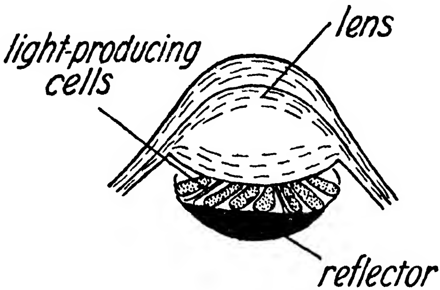


Fig. 27.
Light-producing organ of a crustacean, *Sergestes* (modified after Terao).

is the most efficient form of light production for, unlike all other methods, no energy is wasted in heat formation. Animal light is quite cold.

4 Co-ordination and Regulation

We have seen how impressions are received by the receptor organs and how suitable responses are made by the effectors, it remains to be seen how the stimuli received by the one are transmitted to the other and the multitudinous actions of the organism co-ordinated and regulated.

In the vertebrates which have been more extensively studied than any other group of animals, and also in

the crustaceans, transmission of stimuli is known to take place in two ways, nervous, by the agency of nerves, and humoral, by means of hormones or chemical messengers. Actually the latter may well be the more primitive method while there is evidence, to be mentioned later, that these two methods of transmission are not so distinct as they appear.

In the simplest protozoa, such as *Amoeba*, impulses are transmitted through the protoplasm possibly by chemical means and this also occurs in sponges which have no nervous system. In the more complicated ciliate protozoa they may be delicate fibrils connecting the various groups of cilia with a central body called a motorium. It is possible by the use of delicate apparatus to cut these and loss of co-ordination between the organs they serve invariably follows. The myo-epithelial cells of the hydroids have already been mentioned while all members of the sea anemone and jellyfish group (coelenterates) possess sting cells which react to external stimulus by a direct expulsion of their contents. But in addition to these combined receptors and effectors, these animals all possess a definite nervous system though of a very primitive type. Fine strands of nervous tissue run in all directions, forming

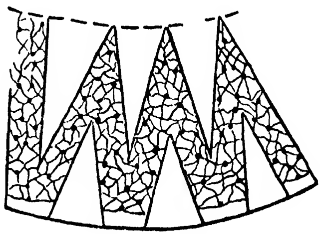


Fig. 28.

Portion of the bell of a jellyfish showing how this may be cut into patterns and the diffuse nervous system will still permit of impulses being carried round.

a diffuse network. Impulses run in all directions with equal ease, for instance a jellyfish may be cut into all manner of patterns, but so long as the continuity of the disc is nowhere interrupted a stimulus given to any part will be transmitted by the nerves and cause waves of contraction which may pass round and round the mutilated disc. A more complicated but essentially similar diffuse nervous system occurs in the sea urchins and starfish, which, like the sea anemones, are radially

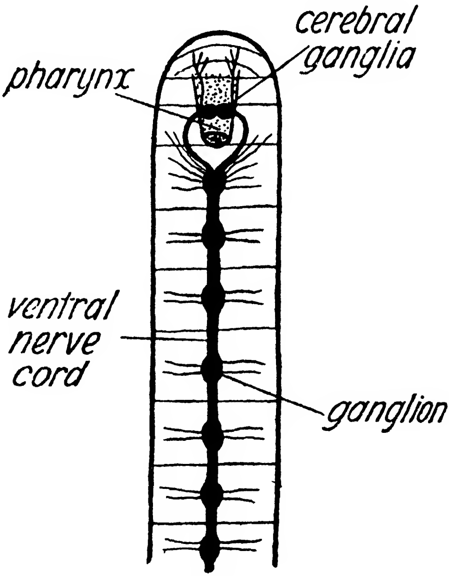


Fig. 29.

Central nervous system of the earthworm showing a series of ganglia, one in each segment, each representing an accumulation of nerve cells.

symmetrical animals which wander about rather than make definite movements in any direction.

As soon as we turn our attention to animals which are bilaterally symmetrical and move in a definite direction with the mouth at or near the front end we find that the nervous system becomes centralized. There is a special accumulation of nervous tissue in the head region, the original association of which with the mouth having led to the development here of sense organs and nerves. From this well-defined nerves pass back into the body. In the higher worms, the crustaceans, insects and spiders, and in the vertebrates, though not in the molluscs, these consist primarily of a stout nerve cord which extends down the length of the body. Unlike the more primitive type the centralized nervous system allows impulses to pass in one direction only, it is polarized.

Each element of the nervous system[1] is called a neurone and consists of a central body containing the nucleus and a series of branching processes called dendrites. One or more of these is usually of very great length and forms the conducting medium or nerve fibre. Though excessively thin these have a definite structure, a central axis cylinder being surrounded by a thin sheath and often, in the vertebrates, by a second fatty covering within this. The latter are known as medullated nerves. Although impulses pass from one neurone to another the fibres never actually touch, but the fine branches in which they terminate interdigitate,

[1] The reader is referred to the volume on *Nerves* in this series for a good introductory account of this very large subject.

the impulse apparently jumping the gap. These connections are called synapses, and it is apparently they which are responsible for the polarity of the nerves, impulses being able to pass the synapse in one direction only. The passage of impulses represents work by the nerve, extremely minute but measurable quantities of oxygen being utilized and carbon dioxide formed. The

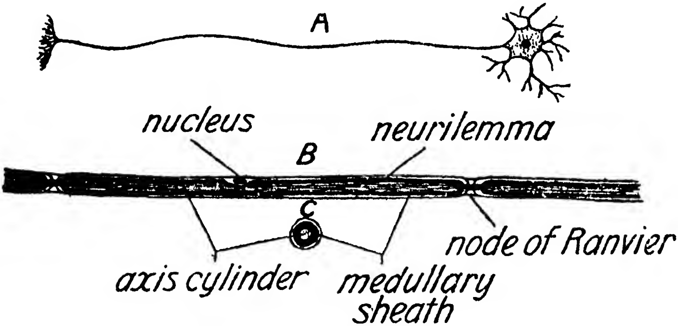


Fig. 30.

A, neurone consisting of a nerve cell with single conducting fibre (unipolar nerve cell); *B*, *C*, longitudinal and transverse sections through a medullated nerve fibre.

speed of conduction varies with the animal and also with the temperature but is not difficult to measure. It ranges from over six hundred metres per second in certain worms, to one hundred and twenty metres in man and less than one metre in the freshwater mussel.

Neurones are of three general types. The sensory neurones receive impulses from the environment either direct or by way of definite receptors while the motor neurones convey these to the different effector organs.

Between the two may be one or many more conducting neurones. Impulses invariably pass in the same direction, from sensory through conducting to motor neurones. This brings us to the subject of reflexes. Many of our actions are involuntary, independent of will and frequently of consciousness. For example, the stimulus of bright light on the retina is followed invariably by contraction of the pupil, and that of food odours on the olfactory organ by the secretion of saliva. We are entirely unconscious of the first and conscious but quite unable to control the second. These are reflex actions; the stimulus received by the receptor is transmitted by way of the sensory neurones to the central nervous system where it is passed on to motor neurones which in their turn transmit it to the effectors which respond in the manner characteristic of them. One event follows another inevitably.

The central nerve cord in animals such as worms or crustaceans is the meeting place of incoming sensory neurones and outgoing motor neurones and also contains conducting neurones which carry impulses up and down, thus uniting the body into a functional unit. The behaviour of such animals is to a large extent made up of simple reflex movements, certain fixed responses being made to definite external stimuli. Such responses in these, or simpler animals down to the protozoa, are called tropisms, thus an animal which always moves towards the source of light is said to be positively phototropic, others which move in the opposite direction are negatively phototropic. This purely mechanical interpretation of animal behaviour is held by a group of

Psychologists called Behaviourists, but though it contains some of the truth it is by no means so certain that it contains all the truth. In many cases a certain response must be made or the animal could not survive, but in other cases there may be alternative responses and the exact behaviour of the animal, at any rate in our present state of knowledge, cannot be predicted.[1]

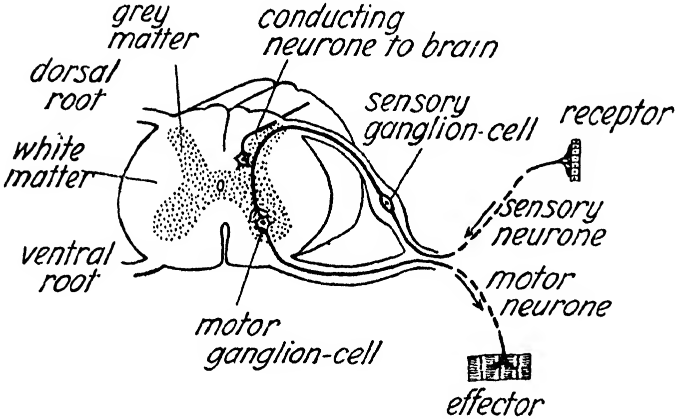


Fig. 31.

Diagram showing structure of the spinal cord and of the roots of the spinal nerves in vertebrates, and the nature of the reflex arc.

In the vertebrates the spinal cord lies within the vertebral column and a pair of nerves are given off through openings between the vertebrae. Unlike similar nerves in the invertebrates these possess two roots, an

[1] The reader is here referred to C. K. Ogden's *A.B.C. of Psychology*, the case for tropisms is most clearly given in *Forced Movements, Tropisms, and Animal Conduct* by J. Loeb and against them in *The Psychology of Animals* by F. Alverdes.

upper (dorsal) root which is swollen and a lower or ventral root. The sensory neurones enter the spinal column by the first of these, the presence of their cell bodies causing the swelling, and the motor neurones leave by the other, their cell bodies being situated in the centre of the spinal column. This is made up of a central mass of nerve cells surrounded by vast numbers of fibres, the greater part of which run longitudinally, the two areas being known respectively as the grey matter and the white matter. The longitudinal fibres not only run between the various spinal nerves but they also communicate with the centre of all nervous activity, the brain.

The brain is the most elaborate and most important organ in the body. To it pass impulses from the major receptors, eyes, ears and nose, which all lie within the head, it controls many of the activities of the body while in it lies the seat of consciousness. As we have already seen the concentration of nervous matter in the head region which has led to the development of the brain was due in the first place to the adjacent presence of the organs of special sense from which it is continually obtaining information about the outside world.

In all the vertebrates there can be distinguished a fore-, mid- and hind-brain, though these vary greatly in complexity and in relative proportions in the various groups. The hind brain is concerned above all things with the co-ordination of movement. It receives messages from the organ of balance and from the innumerable proprioceptors in the muscles and joints and, in accordance with the information they impart,

sends the necessary impulses to the various muscles. The mid-brain contains the optic lobes to which run the optic nerves and it is the visual centre in the lower vertebrates, it is of relatively enormous size in the birds where the power of sight is more highly developed than in any other group of animals. In the mammals visual

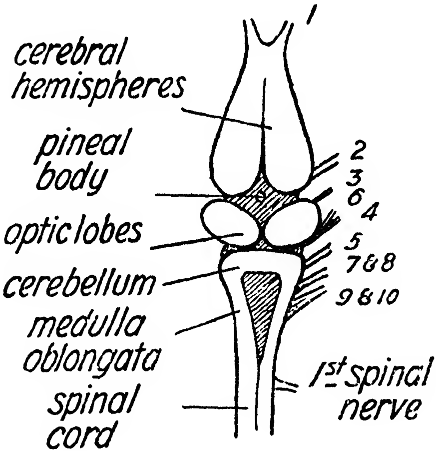


Fig. 32.

Brain of the frog, numbers on the right indicate the cranial nerves.

and other sensory impulses are very largely carried forward to the fore-brain, which in these animals, and above all in man, is greatly enlarged. Here all the sensory impulses, whether they come direct to the brain from the major sense organs in the head or by way of the spinal cord from the body, are brought together and co-ordinated. Originally in fish concerned primarily

with impulses from the olfactory organs, the fore-brain, or cerebrum, in man has become the organ of intelligence and the site of consciousness. The actual nerve cells are situated in the outermost portion or cortex of the cerebrum and to permit of their increase this has become elaborately folded, especially in man where over one thousand million nerve cells are present in the cerebrum. The diverse functions of the body are all controlled by corresponding areas in the cerebral cortex, many of these have been accurately located and gradually the cortex is being mapped out into areas controlling speech, sight, motor activities and so forth.

It has been customary to draw a sharp distinction between reflex, or involuntary, activity and conscious or voluntary activity, with the latter being associated consciousness, memory and thought. Although it has long been recognized that the vast accumulation of nerve cells in the cerebral cortex with their almost infinite cross connections do provide a material basis for higher mental activities, it is only of recent years that these have become the subject of actual experimental study. This is due to the work of the great Russian physiologist, Pavlov and of his pupils on conditioned reflexes, which may briefly be described as the association of one stimulus with another so that the one invokes the response typical of the other. This is far too elaborate a subject to be discussed here, but it certainly represents the beginning of an analysis of the conditions of mental activity, the end of which is far distant and may be equally far-reaching.

A series of nerves enter and leave the brain but, unlike the spinal nerves, these cranial nerves are not more or less equally divided between sensory and motor portions. They are usually either the one or the other, the olfactory, optic and auditory nerves, for example, being purely sensory, concerned exclusively with carrying impulses from the great sense organs to the brain, while others are purely motor, such as three nerves which run to the eye muscles and the far-wandering vagus nerve which plays a large part in the control of the heart, stomach and respiratory system.

In the vertebrates we can distinguish between the central and the sympathetic nervous systems. The latter consists of a double chain of nerves running parallel with and on either side of the spinal cord. It has only slight connections with the central nervous system and its branches run to the viscera and other organs not under conscious control.

The existence of chemical messengers, or hormones, was discovered as recently as 1902, when it was found that the stimulus of food caused the liberation into the blood from the walls of the intestine of a substance later known as secretin. This circulates through the system and, though without action on other organs, causes the pancreas, the principal digestive gland, and possibly also the liver, to secrete. Secretin plays an essential part in the sequence of events which constitutes the process of digestion. Since that date there have been identified a steadily increasing number of similar substances poured into the blood stream in extremely small quantities but with an effect on certain organs or

tissues out of all proportion to their actual concentration in the blood.

We have already had reason to mention one of these, which has been greatly in the public eye of recent years, namely insulin, which controls carbohydrate metabolism. This is produced by islands of cells embedded in the pancreas (but quite distinct from the actual tissues of that gland) called, after their discoverer, the islands of Langerhans. Another very important hormone called thyroxin is produced by the thyroid gland in the neck. It controls metabolism in general, excess of thyroxin in the blood causing oxygen consumption to rise to dangerous heights and people who suffer from hyperthyroidism are in danger of literally burning to death, although they eat abnormally they become excessively thin and very nervous. On the other hand if too little thyroxin is produced (which may be due to a defective thyroid or to too little iodine in the water or food) the opposite condition, known as myxoedema, is produced. The oxygen consumption is much below normal and the patient becomes fat, sluggish and stupid. These two conditions can both be cured, the first by surgical removal of a part of the over-large thyroid and the second by doses of thyroxin.

At the base of the mid-brain lies another gland of internal secretion, the pituitary, formed, as the study of development reveals, not from the brain but from the under part of the head. It is divided into several portions and produces a number of most important hormones. One from the anterior region has a fundamental effect on metabolism and controls growth by

its influence on bone formation. If it is deficient the bones of a child or a young mammal fail to increase as they should and a dwarf is produced, if it is present in excess then the individual becomes a giant. If this increase takes place in adult life when the bones can no longer lengthen, they broaden instead and the very hideous condition, ultimately fatal, of acromegaly is produced. The hinder portion of the pituitary produces a number of hormones somewhat difficult to separate from each other which affect smooth muscle, causing the contraction of the muscles in the smaller arteries or arterioles but the enlargement of the arteries in the kidney and having a most powerful effect on the contraction of the uterus at child-birth. In amphibians a hormone from this region controls the pigment cells, the pituitary being induced to secrete more or less of this hormone by variations in temperature and humidity or in light. In the pigeon it has recently been shown that the production of 'milk' in the crop is controlled by a hormone from the pituitary.

Another hormone which is always present in small quantities in the blood but particularly abundant during periods of strong emotion, such as fear or rage, is adrenalin. This is produced by the central portion of the adrenal glands which are situated above the kidneys. It causes the arteries to contract, thereby increasing the blood pressure, the muscles of the gut to relax, the pupil to dilate and in some cases, for instance man, the hair to stand on end. This last is the result of a stimulation of the so-called pilomotor muscles in the skin. In general its action is the same

as that of stimulation of the sympathetic nervous system. There are other glands, near to the thyroid, called the parathyroids which produce parathyroxin, a hormone which controls the amount of calcium in the blood. Then there is the somewhat mysterious thymus gland which disappears in the adult (its persistence involves certain death), the secretion of which is believed to inhibit the development of the sexual organs. Finally there are the sex hormones, the discussion of which is better left to the next chapter.

All of these hormones are characteristic of the vertebrates which alone possess the glands which form them. Of recent years hormones have also been discovered in the invertebrates, notably ones which control the movements of the colouring matter in the pigment cells of crustaceans, and others which are essential to life in the higher molluscs, such as the octopus and squid.

Hormones are not very complicated substances, indeed, when compared with proteins they are extremely simple, and several of them, notably thyroxin and adrenalin (see the volume on Chemistry in this series), have not only been analysed but also prepared artificially or synthesized in the laboratory. There is reason to think that their function is not essentially dissimilar from that of the vitamins, the one being made by the animal and the other being taken in with the food. Both groups of substances certainly have an effect, due to their peculiar molecular structure, out of all proportion to their actual concentration. A minute dose of thyroxin will bring about the oxidization

of some quarter of a million times its own weight of glucose.

It is impossible, as this very general account may have indicated, to separate the nervous and chemical agencies of co-ordination. The two work hand in hand and are largely dependent the one on the other. Nor are they actually so dissimilar as they appear. It is true that a nervous impulse, which may best be described as a physico-chemical effect transmitted along the surface of a nerve, bears no resemblance to the passage of a substance in solution in the blood stream. There is, however, increasing evidence that the actual effect of a nervous impulse on an effector organ is brought about through the appearance at the nerve ending of a definite chemical substance. For instance stimulation of the vagus nerve causes the heart beat to slacken and it has been found that after such stimulation the substance acetyl choline can be identified in the blood and that exactly the same effect on the heart can be produced if suitably small doses of this substance are injected. There are not wanting those who suggest that a similar secretion, albeit on a very minute scale, takes place at every junction between the nerves, or synapse, which would, of course, be an adequate explanation of the polarity of nerves which is certainly localized in the synapse. The essentially greater importance of hormones is revealed by the fact that organs and tissues can live indefinitely after their nervous connections have been severed, whereas in the absence of certain hormones, such as thyroxin or insulin, which have a profound effect on metabolism, life is impossible.

The results of the complicated machinery of co-ordination are revealed in innumerable and never-ceasing changes and adjustments in the body. Blood is passed in increased amounts to muscles or glands, to the brain or to the gut, whenever these organs demand it, the heart beats faster or slower according to the general needs of the organism, respiration is similarly regulated (through the action of acid on the respiratory centres as we have already seen), also excretion, while in the 'warm-blooded' animals the regulation of body temperature makes constant demands on the various mechanisms which control it.

5 Reproduction, Development and Growth

We have been concerned so far with the organism as an individual and with the more important of the means whereby its identity is maintained, with the nature, it may not inaccurately be described, of the vigilance which is the price of life. But the organism is something more than an individual, than an isolated unit of living matter, it is also a member of the race to which it belongs and the link between its ancestors and its descendants, having arisen from the former and giving rise, in its turn, to the latter. The process of reproduction and the ensuing ones of development and growth, all fundamental characteristics of living matter, must now claim our attention.

Reproduction is usually associated in our minds with sex. We know that reproduction in ourselves and in all animals with which we come normally in

contact, is invariably preceded by sexual intercourse and that the production of seeds by plants is the result of similar processes. Nevertheless every good gardener knows that many plants can be propagated by cuttings and that this is, indeed, often the easiest method of obtaining new plants, while a study of botany reveals that some such process is the normal, and often the only, method of reproduction in many plants.

This asexual, or vegetative, mode of reproduction is far from uncommon in animals. The simpler protozoans, such as *Amoeba*, when they have attained a certain size reproduce themselves by a process of simple division (simple in name only for we know nothing of the underlying mechanisms), the place of the original animal being taken by two smaller, but otherwise similar, animals. Certain sea anemones divide into two or else 'fragment', the small pieces detached in the latter process all developing into normal anemones. The hydroids form large colonies consisting of branches on which new animals or 'polyps' develop. Little jellyfish or medusae are budded off, which swim away and on these alone the sexual organs develop. The massive colonies formed by corals are due to the repeated divisions of the individual polyps. Many worms normally break up into an ordered series of pieces, each of which is capable of developing into a normal worm, while even in the sea squirts, which are allies, though degenerate ones, of the vertebrates, asexual reproduction by buds is of frequent occurrence.

This mode of reproduction is associated to a large extent with the power of regeneration. It is well

known that it is useless attempting to destroy earthworms by cutting them into pieces, for each of these may regenerate the lost parts and form a new worm. An almost unlimited power of regeneration is possessed by the simpler flatworms and by many of the sea anemone group. A starfish will regenerate lost arms, a single arm with a sufficient portion of the central disc being capable of growing into a normal animal. With the increased specialization of the tissues in the more highly organized animals this power of regeneration decreases, being confined to the growth of new limbs in crustaceans and in amphibians and of new tails in lizards, and merely to the formation of new skin in ourselves.

Sexual reproduction involves the setting aside in the body of the animal of definite reproductive cells. These gametes, as they are known collectively, are of two kinds, the one, typically large and incapable of movement, being the eggs or ova (ovules in plants), and the other, typically small, very numerous and active, being the spermatozoa (spermatozooids in plants). The organs in which they are produced in animals are known collectively as gonads, ova being produced by ovaries and spermatozoa by testes. In the more highly organized animals the individual usually possesses either the one type of gonad and its associated structures or the other, if it has ovaries it is a female and if testes a male. In many of the simpler animals and also in the common snail and its allies and a few other comparatively complex animals, individuals are not of separate sexes but are hermaphrodites with both ovaries and testes, or a complex of the two called an ovo-testis.

In the plants separate sexes are the exception. In certain animals though only eggs or sperms are produced at any definite time the product of the gonad alters, frequently the animal starts sexual life as a male and then becomes a female, although the reverse may occur, while certain bivalves, notably the 'native' oyster, *Ostrea edulis*, produce first sperms, then eggs, then sperms again and so on, the speed with which the manifestation of one sex succeeds that of the other depending on the temperature.

The spermatozoa of the majority of animals, including all the vertebrates, resemble excessively small tadpoles, with a rounded head which contains the all-important nucleus and a long, motile tail which is the organ of locomotion. In a few groups, such as the crustaceans and roundworms, they are much larger and have an irregular or star-like appearance. Although it is only in these last, rather unusual cases, that the spermatozoa are anything but exceedingly numerous, the number of eggs produced varies very greatly not only between different groups but in different species within the same group. There is a perfectly clear connection between the number of eggs produced and the chances of fertilization and of survival of the new individual thereby initiated. Thus animals which discharge their eggs freely into the sea there to be fertilized by spermatozoa discharged by the males, such as starfish, sea-urchins, bivalve molluscs, and the majority of bony fishes, produce these in immense numbers. It has been calculated that the American oyster, *Ostrea virginica*, may discharge over one hundred

million eggs during one spawning period, of which there may be five or six in the course of a year. Other animals, notably the univalve molluscs, the octopus and squid, and the higher crustaceans, produce fewer eggs which are large owing to the greater amount of yolk or food reserve they contain. These are fertilized within the body of the parent, usually as the result of copulation between the male and female, or between two similar individuals in the case of the hermaphrodite snails, and are then surrounded by a protective coat before they are laid. Though fewer in number than the first type, they are protected during development and hatch out as small animals with a fair chance of survival. The largest eggs are those of birds, where an immense amount of yolk is present. In this case parental care adds to the chances of survival, in the reptiles such care is unknown and the eggs, though very similar to those of birds, are much more numerous.

Finally the egg may be retained in the body after fertilization. In the simplest cases the body of the parent merely takes the place of a protective capsule, the young being born when the yolk is exhausted. But in the highest type of viviparity, which is one of the essential characteristics of the mammals, the developing embryo comes into intimate contact with the body of the mother from which it is nourished. The need for yolk no longer exists and the chances of survival of the young, assisted also as they are by parental care for a considerable period, is very great. Hence though the eggs of mammals are extremely small they are also very few in number, the material for development which

the bird puts into the egg being supplied direct to the developing embryo by the female mammal.

The gametes are fundamentally unlike other cells of the body. This has to do partly with their nuclear constitution which will be discussed in the next chapter. The egg possesses the capacity for developing into an organism essentially similar to the one which produced it, but it must first be activated or fertilized. This is usually brought about by the entrance of the male gamete, but in some instances the egg proceeds to develop without the stimulus of such a union. This condition is known as parthenogenesis (Greek, *parthenos* = virgin, and *genesis* = descent), and is not at all uncommon in the rotifers or wheel animalcules, in the simpler crustaceans and in certain groups of insects. Frequently there are a series of parthenogenetic generations followed by a sexual generation the products of which may be especially fitted for surviving the winter. In the honey bee and the common wasp eggs which develop parthenogenetically give rise to males and those which are fertilized to females. In the Indian stick insect, *Dixippus*, the eggs apparently always develop parthenogenetically; males do occur but they are extremely rare and mating has never been observed.

Experimental studies of fertilization, largely carried out with the eggs of sea urchins and starfish, which form admirable material for this purpose, have shown that this can be induced artificially in one hundred per cent of cases by immersing the eggs successively in appropriate solutions. The significant factors are first a

temporary increase in the permeability of the egg membrane, brought about by some fat solvent such as a fatty acid, and then a removal of some of the water from the interior by a high concentration of salts, or of some inactive substance such as sugar, in the surrounding sea water. There is good reason to think that the actual activation of the egg by the sperm is the result of similar changes in the egg.

But fertilization by the sperm consists of more than the actual activation of the egg, which, as we have seen, can be accomplished artificially and can also in some cases be produced by the sperm of some other animal. The sperm attaches itself to the surface of the egg, provoking thereby the formation of a fertilization membrane around this which, amongst other things, prevents the entrance of other sperms. The head or nucleus of the sperm then enters the cytoplasm, the tail being discarded, and the nuclei of the two gametes approach each other and eventually fuse. This conjugation transforms the egg into a zygote which, in the great majority of animals, is the first stage in the formation of a new individual which develops directly from it. Conjugation is found even in protozoans. In certain cases the process of simple fission may be interrupted from time to time by conjugation, two individuals uniting temporarily and exchanging portions of their nuclear contents and breaking apart to resume, with renewed energy, their reproductive activities. Still more complex protozoans, of which the malarial parasite is a good example, produce at one stage in their complicated life-histories two types of individuals,

the one small, numerous and very active like sperms, and the other larger, less numerous and passive, like eggs. These unite permanently by a process usually called syngamy and thereby initiate a new life-cycle. In other cases these protozoan 'gametes' are identical in appearance although conjugation only takes place between individuals of different origin. The purpose of conjugation is not quite so clear as it is often stated to be. It certainly ensures the blending of hereditary substance from two sources, the mechanism of which will be described in the next chapter, but that this is not essential for the development or the maintenance in nature of the individual is revealed by the frequence of parthenogenesis. There remains, however, the probability that the continuance of evolution in any group is dependent upon, at any rate, the occasional occurrence of conjugation.

All multicellular organisms, therefore, no matter how simple or how complex, how small or how large, when they reproduce sexually must begin life as a single cell which contains within itself the potentialities of the future adult no matter how complex this may be. The study of the development of the activated egg or zygote is known as embryology and constitutes one of the most interesting branches of biology. The care and patience of innumerable investigators during the past century have furnished science with most detailed descriptions of every stage in the development of a great number of widely diverse animals. It is impossible here to give even the briefest summary of these and we must confine our attention largely to one group, the vertebrates,

and to statements of general application to the development of metazoans.

The immediate effect of fertilization, of the first contact of the egg with the sperm and not of the later penetration of the egg, is a remarkable increase in metabolism. Oxygen consumption and the resultant liberation of carbon dioxide may rise by as much as eight thousand per cent! After the nuclei of the two gametes have fused there is a short period of nuclear adjustment and then the zygote divides. The period of cleavage or segmentation has begun. The nature of this cleavage, or division of the zygote into a number of cells, depends on the amount of yolk present, if there is little yolk the zygote first divides into two equal hemispheres and then four equal cells and so on in regular sequence, but if there is a great deal, the hen's egg is the best example of this, cleavage is confined to a small area at one side and for a long time the developing embryo lies upon the surface of the yolk which it gradually consumes. Cleavage proceeds, nuclei dividing regularly and the cytoplasm as regularly as yolk permits until a compact mass of small, rounded cells, simple and undifferentiated, appears. At this stage a central cavity normally forms and the developing organism assumes the form of a hollow sphere and is known as a blastula (see Fig. 33).

There follows an infolding of one side of this sphere which leads to the obliteration of the original cavity and the formation of a new sphere with a double wall and an opening at one side. This stage is known as a gastrula and it marks the beginning of the organization

of the embryo. The cells which are tucked inside are called the endoderm to distinguish them from the surrounding ectoderm, while between the two there develops a third cell layer known as the mesoderm. These 'germ layers' though realized to be less

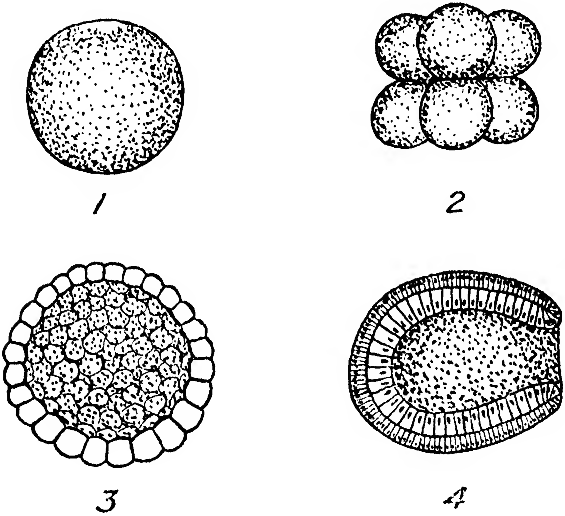


Fig. 33.

Stages in the development of *Amphioxus*, a very simple chordate. 1, egg; 2, eight-cell stage; 3, blastula; 4, gastrula with external ectoderm and internal endoderm due to infolding, the opening is the blastopore, the upper margin being the dorsal lip.

instrinsically important than they were once considered are still of great convenience in describing the course of development.

The developing organism has now reached the stage when the organs begin to be blocked out, as it were, in

the rough. Of these the gut and its associated structures arise from the infolded endoderm, the original opening usually forming the anus, a perforation at the other end forming the mouth a little later. The notochord or primitive axial skeleton of the vertebrates also arises from the endoderm. The skin and the nervous system and sense organs, all those parts of the organism which are concerned with the external world serving for

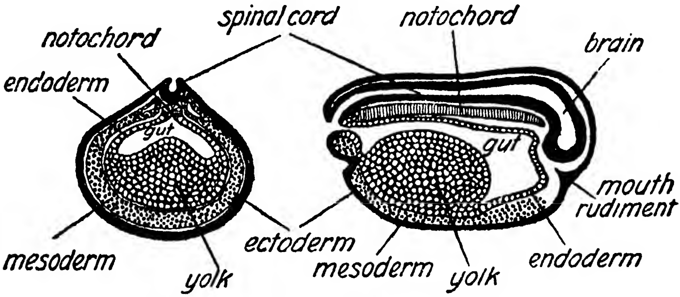


Fig. 34.

Transverse and longitudinal sections through developing embryos of a frog at the time when the organs are being "blocked out", transverse section somewhat earlier than the other (after Marshall).

protection or the reception and transmission of stimuli, are formed from the ectoderm, while the intermediate organs, notably the circulatory, excretory and reproductive systems and the bulk of the skeleton, are formed from the intermediate mesoderm.

When they first appear these structures are but the forerunners of the organs into which they develop. They are composed of unspecialized cells incapable of carrying out the functions of the fully formed organs.

The next stage in development is the alteration or differentiation of these cells into specialized tissues. The cells of the embryonic nerve cord become nerve cells with all the highly complex and characteristic properties of such cells, the cells of the embryonic gut become capable of secretion or of absorption according to their eventual destiny, muscle cells appear, cartilage cells surround the notochord, to be followed later by bone, the circulatory system develops and with it blood cells which circulate through the body as soon as the heart begins to contract. All the essential organs are constituted and become capable of playing their part in the life of the organism. The embryo, in short, becomes a self-supporting organism.

The time taken to attain independent existence varies according to the amount of yolk originally present in the egg (except in viviparous animals where the embryo is nourished by the mother). The more yolk there is the more highly developed will be the organism when it is first thrown on its own resources. Thus a bird or a reptile spends a relatively long time in the egg before it hatches out and when it does so it is in all essentials a small adult. In many animals this is far from being the case; the yolk is used up long before the embryo can attain such an elaboration of structure and it hatches out as a free-living organism but quite unlike its parents. Such independent and free-living embryos are known as larvae. A frog tadpole is the best-known example, but it is only one of very many, for the great bulk of crustaceans, molluscs, marine worms, starfish and sea-urchins, pass through a larval

stage which only the eye of experience recognizes as the young of totally different adults. Where the yolk is very limited larvae may develop very quickly and in certain sea squirts (see Fig. 48, p. 212) a fully formed tadpole (so-called owing to its resemblance to a larval frog), with brain, sense organs, gut, muscles and

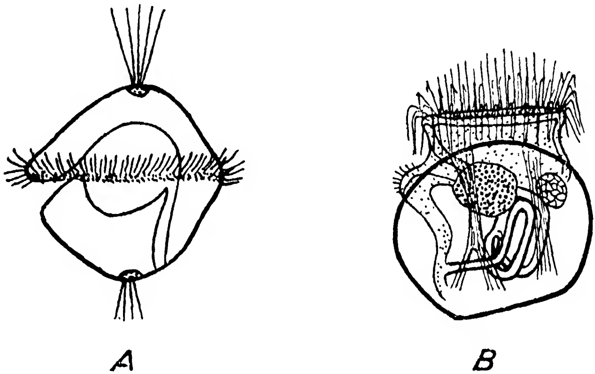


Fig. 35.

A, trochosphere larva of an annelid worm; *B*, veliger larva of an oyster.

notochord, may be formed at the end of six hours after the fertilization of the egg.

Larvae feed voraciously and grow correspondingly quickly until they attain the necessary size and have accumulated the necessary reserves of food to enable them to change into the adult, a process known as metamorphosis. This frequently involves a radical reorganization of the whole structure of the body, yet it is usually carried through in a remarkably short time.

Examples of metamorphosis are afforded by the conversion of a tadpole which is adapted for life in water to a frog which lives on land, of a free-swimming 'veliger' larva into an attached oyster, of the round freely-swimming 'trochosphere' larva into the elongated bottom-living worm.

The next stage in development is concerned solely with growth. The juvenile animal feeds and grows, gradually attaining the size of the adult. The beginning of adult life and the attainment of maximum size, however, seldom coincide. The criterion of the former is sexual maturity and this is usually attained, as in man, before growth is completed. Certain animals indeed, such as fish, apparently never cease growing, although this becomes slower and slower with advancing age, but others, such as the mammals, stop growing only to the full ossification of the bones, some time after sexual maturity has been reached. After this there is a period, often of considerable length compared with the earlier stages, of quiescence. The organism no longer grows but it maintains and reproduces itself. Finally a period of old age ensues when reproduction may cease and the previous stability is lost, the processes of maintenance and repair become increasingly difficult and death follows. Death is one of the prices paid for specialization and is unknown in the protozoans when the individual divides into two others and so is potentially immortal.

Such in very brief outline is the course of life from the zygote to reproduction and eventual death. Development has been well described as a series of

responses to stimuli, the responses being "not merely repetitive, as in the case of tissue cells, but progressive", and the egg likened to a complicated machine "so constructed that it transforms itself at every critical stage into another machine with its own peculiar modes of action" (E. G. Conklin). The nature of the mechanism of this continuously changing machine is one of the major problems of biology.

The process of development would be easier to understand if precursors of the various organs could be identified in appropriate regions of the egg. This is actually the case in the so-called 'mosaic' eggs of sea-squirts, worms and molluscs. If such eggs be fertilized and then, after the zygote has divided several times, the cells are separated, as they can be by appropriately delicate technique, each of these continues to develop for some time and to form that part of the embryo to which it would have given rise had it remained in contact with the other cells. Cleavage in this case is said to be *determinate*. The parts of the future embryo are roughly blocked out in the egg and so become localized in different cells as cleavage proceeds.

But these mosaic eggs are greatly outnumbered by the 'regulative' type in which there is no initial organization of substances in the egg. When early cell stages are separated they develop not into portions of the embryo but into complete, though small, embryos. Two zygotes may be induced to adhere to each other and will then give rise to an embryo twice the normal size. Cleavage here is called *indeterminate* because it does not divide the developing zygote into cells

which are the inevitable precursors of definite portions of the differentiated organism. There is some regulative mechanism present in these eggs and in the cells formed during cleavage which ensures that a normal embryo shall be formed out of the material available, even though this is reduced or augmented artificially.

Of recent years some very beautiful experiments on amphibians by a German zoologist named Spemann have revealed that even in the blastula there is no specialization of the cells ; they may be removed from one place and grafted on to another without in any way affecting the harmonious development of the embryo. But a stage is reached in development when the cells are no longer all potentially capable of forming any of the future organs or tissues. They become specialized, chemically but not structurally for this stage in differentiation has not yet been reached. This initial specialization follows the first appearance of the infolding 'lip' of the gastrula, in which is localized what Spemann has called the 'organizer'. The influence of this gradually extends over all the hitherto unspecialized, equipotential cells. After the appearance of the organizer, cells which, owing to their position, are known to be going to form the central nerve cord will inevitably do so even though they are grafted on to portions of the gastrula where the nerve cord could never normally appear. Yet these identical cells if they had been moved and grafted immediately before instead of immediately after the organizer appeared would just as inevitably have aided in the production

of the particular tissues which are normally produced by the region on to which they were grafted.

Still more recently it has been found that the organizer is a chemical substance, that it can be extracted by suitable reagents from the cells in which it appears, and that this extract can be used successfully to induce the formation of a primitive nerve cord in portions of the gastrula where it never normally develops. This represents a distinct step forward in the elucidation of the mechanism underlying development.

Once differentiation has begun the fate of any cell, whether it develop into muscle or gland, retina or nerve, skin or bone, appears to depend on its position in the embryo. This is borne out by the results of work on tissue culture. In 1910 an American biologist, Ross Harrison, perfected a technique which enabled him to cultivate tissues under artificial conditions altogether apart from the body of which they had originally formed a part. This sub-science of tissue culture has developed greatly since that date and produced a quantity of very important knowledge. It has revealed that the various tissues are dependent on one another, for if they are isolated they lose their characteristic form. Thus kidney tubules when cultured outside the body together with fragments of connective tissue (the supporting and packing tissue of the body) which normally surrounds them, continue to live and do not change. But in the absence of this connective tissue the very highly specialized kidney cells lose their characteristic appearance and gradually become like the

unspecialized cells of the embryo. But if connective tissue be added to this undifferentiated mass of cells the opposite process takes place and the tubules are reformed.

The reverted tissue has another property in common with embryonic cells, that of rapid multiplication. Specialized cells, such as those of the kidney, lose this power for fully developed organs, maintain themselves but do not normally increase. Loss of specialization and rapidity of increase is characteristic of malignant growths such as cancer, and if these are cultured artificially in the absence of other tissues, they continue to divide and grow without alteration, showing that they are actually reverted or embryonic tissue. There are also certain so-called benign growths in which the tissues remain specialized and grow more slowly and these when cultured alone lose their specialization, divide more rapidly and become indistinguishable from malignant tissue.

In the same way, apparently, as the tissues of the developing organism become specialized they interact the one upon the other, the essential characteristics of one tissue being maintained by some substance produced by another tissue which is itself influenced by the first. We can conceive of the chemical organizer as initiating a series of exceedingly complex chemical reactions which cause the ever-increasing specialization of the embryo and culminate in the establishment and maintenance of the adult organism, any breakdown in this stage involving the appearance of malignant growths fatal to the organism.

The influence of hormones on the development and growth of vertebrates is profound. This is most strikingly displayed in the metamorphosis of amphibians from the tadpole larva to the terrestrial adult. The blood must contain a certain concentration or 'threshold value' of thyroxin before metamorphosis can occur. It will be recalled that iodine is an essential constituent of thyroxin and it follows that if the tadpole is prevented from obtaining this element it cannot produce thyroxin. Under such conditions it fails to metamorphose but grows into an abnormally large tadpole. This actually occurs in nature for the well-known axolotl of Mexico is really the larval stage of a terrestrial amphibian named *Amblystoma*, but may continue throughout life in the larval condition because the necessary threshold value of thyroxin is never attained. The larva continues to grow and becomes technically an adult in that it attains sexual maturity. A tadpole may be induced to change into a frog at an abnormally early age if it is fed on pieces of thyroid gland (from any source, for the secretion of the thyroid is the same from fish to mammals), or additional iodine is added to the water, and the same treatment will cause an axolotl to transform itself into an Amblystoma.

The higher vertebrates undergo no such sudden change during growth and the effect of thyroxin cannot be demonstrated in so spectacular a fashion but it is every bit as important, indeed still more so in the warm-blooded vertebrates as revealed by the very serious effects of thyroid deficiency or excess described in the preceding chapter. The effect of the pituitary is

fundamentally even greater than that of the thyroid for in addition to exerting its own specific effect on bone formation it controls the thyroid which fails to function in its absence.

The chromosomal constitution of the animal (see next chapter) determines its sex, that is which of the alternative gonads, ovary or testis, shall develop. These in their turn, by virtue of the sex hormones which are elaborated within them, control the secondary manifestations of sex. These are all-pervading, including differences in the rate of respiration and of the pulse and in the metabolism generally, as well as the obvious external differences such as the presence of a comb and spurs in cocks, of horns or antlers in many male ungulates, of hair on the face of men, and of the external reproductory apparatus in mammals generally. Removal of the gonads, particularly in young mammals, leads to striking changes in appearance and behaviour, while the substitution of the gonads of the opposite sex produces corresponding changes in the secondary sexual characters. A male guinea-pig into which ovaries have been grafted in place of the original testes may actually suckle young. A complete functional change of sex is impossible in mammals after birth because the accessory organs of reproduction have developed too far to permit of their being completely remodelled, but this can apparently happen under natural conditions in birds.

Growth does not necessarily involve increase in size, animals may grow smaller as well as larger. This does not apply to animals as highly organized as

vertebrates where the firm skeleton and the delicate equipoise of organs and tissues render this impossible. But in many of the simpler animals a decrease in size is a perfectly normal happening. Certain sea squirts, for example, spend the winter in the form of small white masses in which the organs of the normal animal, indeed organized tissues of any kind, are absent. The animals have grown smaller and also lost the differentiation which is one of the chief fruits of growth. In the spring the process is reversed, the white mass grows and the organs are re-formed. It is possible by starving a jellyfish to make this grow smaller and smaller until it finally becomes a small spherical mass. Sea anemones and flatworms respond to starvation by becoming smaller and smaller, but they retain the normal proportions of the body.

It would appear, therefore, that the increase in size and the differentiation of cells and tissues which constitutes development is not an irreversible process, but that if the organism is sufficiently simple in organization, like a jellyfish or a flatworm, or sufficiently plastic like the more complex sea squirt, the process may be reversed, involving decrease in size and 'dedifferentiation'. The mechanism underlying the latter process forms an interesting subject for speculation. It would appear as though, in the absence of adequate nourishment for the tissues, chemical control of differentiation is lost enabling the cells to revert to the embryonic, equipotential condition from which the adult organism can quickly be reformed when conditions again become favourable.

6 The Mechanism of Inheritance

No aspect of biology has excited the interest of humanity more than inheritance; the problem of why like produces like has vexed man from the earliest times. The substitution in this subject of exact knowledge for vague surmise and legendary belief represents the greatest achievement in biology during the past half century. When Charles Darwin published the *Origin of Species* in 1859 he was without any accurate knowledge of the mechanism of heredity which he refers to as "the strong principle of inheritance". To-day genetics, as the science of heredity is usually termed, can rightly be described as a most exact branch of biology. We owe this great advance in the first place to an obscure Bohemian Abbot named Mendel, whose work, ignored and forgotten for more than three decades, was brought out of its obscurity and awarded fitting recognition at the beginning of the present century. Mendel's triumph lay in his mode of attack. Instead of regarding the organism (his work was entirely with plants) as a whole, he selected definitely contrasted characters and by experimenting on these discovered that they were inherited according to definite rules and quite independently of other characters. He was the first to analyse inheritance and met with the success which rewards pioneers.

Before proceeding to an account of Mendel's work and of the more recent developments from this, it will be advisable if we first discuss what we have so long neglected, the actual process of cell division for in this

we shall find the material basis for heredity. The discovery that the great bulk of plants and animals were made up of vast numbers of cells led naturally to an intensive study of these structural units of living matter, and in this way the sub-science of cytology developed. Attention soon became focused upon the nucleus and especially on the contained chromosomes and their remarkable behaviour during cell division. It was first realized in 1903 that the behaviour of the chromosomes as determined by the cytologists provided an explanation for the laws of inheritance established by Mendel and his successors. Since that date these two branches of biology which originated independently have advanced very largely hand in hand. The great multiplicity of sub-sciences in biology is evidence of its immaturity for the advance of science is always attended by an increasing simplification as the emergence of general principles brings order into the original welter of miscellaneous and apparently unrelated facts. We are therefore justified in saying that biology made a great step forward when cytology and genetics joined hands.

In the introductory remarks about the general properties of living matter reference was made to the darkly staining masses called chromosomes in the nucleus. These may justly be described as the most important bodies in the living organism. They occur in every cell in every plant and every animal and are absolutely characteristic in number and shape for every species. They range in number from four in *Ascaris*, a common parasitic roundworm, to one

hundred and sixty-eight in the brine shrimp, *Artemia*, man coming in between with forty-eight. Moreover careful examination reveals that the individual chromosomes vary characteristically in size and shape and invariably consist, with the notable exception of the gametes as will be shown later, of *two sets*. For instance, should an animal possess six chromosomes, two of these may be rounded, two elongated and two hook-shaped.

The chromosomes appear, by which is meant that they can be stained, immediately before cell division. During the resting period between divisions they cannot be identified as discrete bodies within the nucleus but we are justified in believing that they retain their identity even when they cannot be stained, because at every cell division they appear in precisely the same numbers and with precisely the same shapes. Apart from the very rare occasions when it divides by a simple elongation followed by a constriction in the middle, a process known as amitosis, the nucleus divides by the very beautiful and exact process of mitosis.

The onset of cell division sees the condensation of the chromosomes from the fluid state in which they apparently exist in the resting nucleus and at the same time the centrosome or attraction sphere, a star-shaped body which lies in the cytoplasm at one side of the nucleus, divides into two, the two parts arranging themselves on opposite sides of the nucleus. Meanwhile the nuclear membrane breaks down and fibres radiate out from the centrosomes uniting in the middle to form a spindle-shaped aster. The chromosomes, no matter how numerous they may be, now arrange

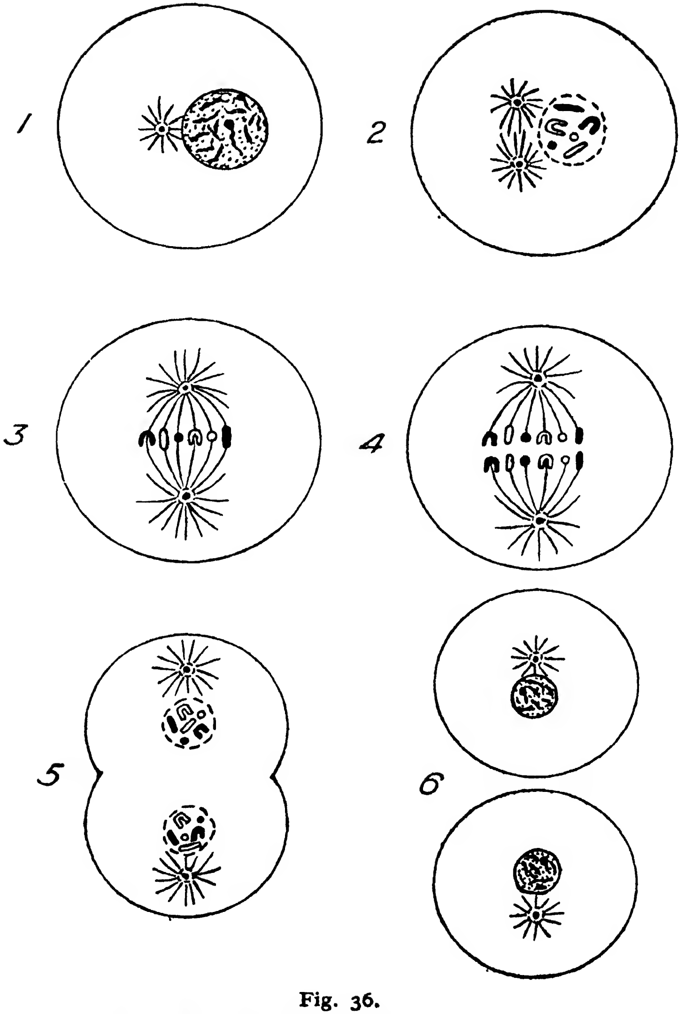


Fig. 36.
Stages in cell division, explanation in text.

themselves in the equatorial plate where the two sets of fibres meet. They then split each one longitudinally and the halves travel to opposite poles. They then resume the resting condition while the nuclear membrane reforms and the cytoplasm, following the lead of the nucleus, also divides. The centrosomes persist but remain quiescent until by their preliminary division they again initiate that of the nucleus.

This very exact mechanism which operates, with a few rare and rather doubtful exceptions, whenever any cell of any plant or any animal divides, ensures that every cell in the organism possesses the same number and the same two sets of chromosomes. Even before the chromosomes were recognized as providing the physical basis for heredity, the exact manner of their division was sufficient to indicate their fundamental importance to the organism.

It will be recalled that when an egg is fertilized by a sperm the former is not only activated but the nuclei of the two gametes fuse. It is clear that if two ordinary nuclei united the number of chromosomes would be doubled, yet we know that the chromosomes of every generation of the same species are identical in number and form. This is so because the nuclei of the gametes, both egg and sperm, contain only half the normal number of chromosomes, they possess *one* set instead of two. During the elaboration, or maturation as it is called, of the gametes in the gonads there is a ' reduction division ' when the chromosomes instead of all lying side by side in the equatorial plate, arrange themselves in pairs, like to like, and then separate, one complete

set consisting of half the normal number of chromosomes, passing to each of the poles. There is always a second, normal division after the reduction division before the gametes are actually mature, the final result being four similar sperms in the testis but only one egg of the ovary, the other three cells in this case consisting of nuclei with the minimum of cytoplasm. These are known as polar bodies and invariably degenerate. This difference between the formation of the two kinds of gametes is difficult to understand though it may be due to the necessarily greater amount of cytoplasm in the

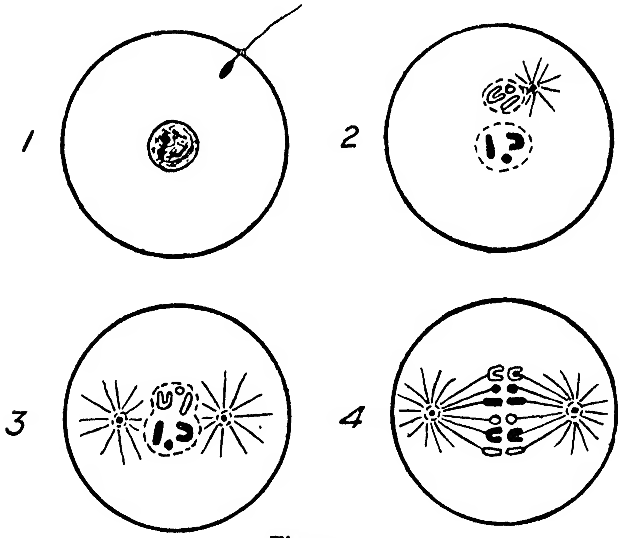


Fig. 37.

Fertilization of an egg by a spermatozoon, fusion of the nuclei of the gametes and the beginning of the first division of the zygote. The centrosome enters with the sperm.

egg which will be assisted by the unequal division of this.

Thus it comes about that when the nuclei of the gametes fuse at fertilization two single or 'haploid' sets of chromosomes, one from the paternal and the other from the maternal parent, unite to form the 'diploid' nucleus of the zygote from which all the nuclei in the adult body eventually arise. On the basis of their chromosomal constitution there are thus two types of individuals, gametes and zygotes, each being usually further divisible, as we shall see later, owing to differences in their contained chromosomes.

We are now in a position to consider the mechanism of inheritance. By crossing organisms with contrasted characters, for instance peas with long and short stems, Mendel discovered that the offspring, the first filial or, as this is usually expressed by geneticists, the F1, generation consisted exclusively of plants with long stems. Tallness, in his words and the expression has been retained, was *dominant* over the *recessive* shortness. The further breeding of members of the F1 generation gave striking, but entirely consistent, results. Instead of these tall plants giving rise, as would their tall parents, exclusively to tall offspring, approximately 75 per cent were tall and 25 per cent short. Still further inbreeding of this F2 generation revealed that all the short individuals produced short offspring, they invariably bred true, but that only one-third of the tall individuals bred true, the remaining two-thirds producing the same 3 : 1 ratio of tall and short individuals as did the F1 generation.

Mendel obtained the same perfectly consistent results with seven sets of contrasted characters on which he worked. After careful consideration of these he propounded three laws. The first, and by far and away the greatest of these, he called the Principle of Segregation, and this has been well described as corresponding in the sphere of genetics to the atomic theory in chemistry. Mendel considered that the various characters of the organism, such as those he chose for experimentation, were represented by definite units or 'factors' as he termed them, in the body, and that, though these might be mixed in the parents they invariably segregated out in the gametes which could not be other than pure for any factor. How this comes about is plain enough to us in view of the behaviour of the chromosomes during the maturation of the gametes, but Mendel knew nothing of this; his laws were purely empirical, the only possible way in which he could account for his experimental results.

Innumerable breeding experiments on both plants and animals have confirmed Mendel's results over and over again and established beyond all question the truth of the Principle of Segregation, for which the discoveries of the cytologists have provided the necessary material basis. Let us now regard Mendel's experiments afresh in the light of modern knowledge. The original individuals were of pure stock, when bred amongst themselves all tall plants produced tall offspring and all short plants short offspring. They were what we now call *homozygous* for the factor controlling length of stem. This factor, for reasons given later, is

almost certainly located in a certain region of a certain chromosome, or rather in the same region in the similar chromosomes of the two sets present in the zygote. Accordingly when the gametes are formed and one set of chromosomes passes into each of these, they will all be alike for that particular factor and when they unite to form zygotes all of these will be homozygous for that factor. But when peas with long and short stems are crossed then gametes containing the factor for the long stem will fuse with those containing that for short stem

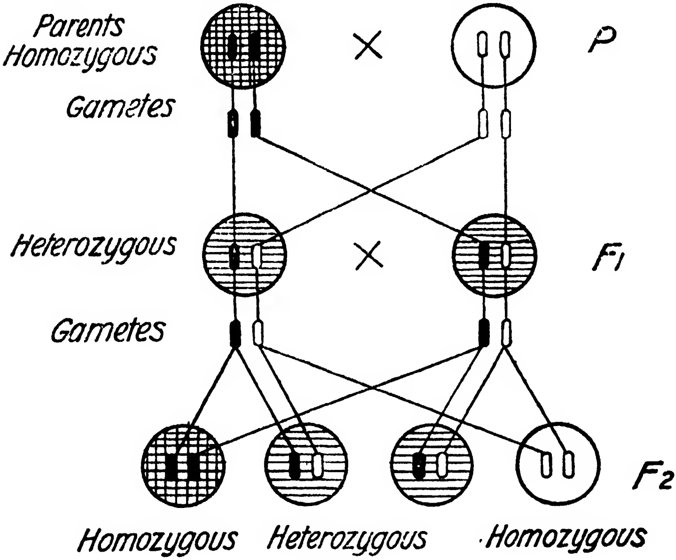


Fig. 38.

Diagram illustrating the mechanism of Mendelian inheritance and the Principle of Segregation. The genes are represented by oblong bodies.

and the zygote so formed with the individual into which it develops will be *heterozygous* for the factor controlling length of stem. One of the particular pair of chromosomes will possess the factor for tallness and the other the factor for shortness.

Since long stem is dominant over short stem the apparent result will be normal long stemmed plants. But the true state of affairs is revealed when these F1 individuals are crossed with each other. Each plant will produce gametes with *either* the chromosome bearing the factor for tallness *or* the chromosome bearing the factor for shortness. The factors will, as Mendel said, segregate in the gametes. There will thus be two kinds of eggs and two kinds of sperms and, the laws of chance ensure that the two types of female gametes stand an equal chance of being fertilized by either of the two kinds of male gametes. As shown in Fig. 38 the result will be that each type of egg will give rise to zygotes half of which are homozygous and half heterozygous, the total result being one quarter individuals homozygous for tallness, one quarter homozygous for shortness and one half heterozygous. But these last, owing to the dominance of tallness, will all develop into tall individuals so that the apparent result will be one quarter short individuals and three-quarters tall ones. Only further breeding experiments will reveal which of the latter are actually homozygous for tallness, all breeding true, and which are heterozygous, giving the same 3 : 1 ratio as before.

Dominance is not of universal occurrence. The heterozygous nature of the F1 generation is better

displayed in crosses where the contrasted characters involved do not exhibit dominance and recessiveness. Such an example is provided by crossing certain breeds of white and black fowls which produce in the F1 generation the so-called Blue Andalusian, which is intermediate in colour between the two parents. If these Andalusians are bred with each other the offspring consists of one-quarter white, one quarter black (both homozygous and so breeding true), and the remaining half Blue Andalusian (heterozygous and producing when bred the same 1 : 1 : 2 ratio).

So much for the law of segregation, the purity of the gametes, the fundamental principle of genetics. Mendel went on to state another law to the effect that if organisms with several different sets of contrasted characters were crossed with each other these characters were inherited independently of each other. The different pairs of characters, in other words, segregated independently. This is not a law of the same standing as the first, for though true within Mendel's limited experience it is not universally so. To the extent that it is applicable it is of the greatest practical value to the breeder, enabling him to combine useful characters from a variety of individuals into one individual. It is in this way that new varieties of wheat have been produced capable, for instance, of resisting drought or rust fungus and yet giving a high yield of grain.

But if Mendel's second law has been found to be only of limited application, his third law, that of 'unit characters', has completely failed to stand the test of time. This also is due not to any faultiness in Mendel's

reasoning but to the insufficiency of his experimental data. It so happened that the seven pairs of contrasted characters with which he worked all behaved as though they were units, as though they were controlled by single pairs of factors. Modern research has shown that probably no character is controlled by only one factor on the chromosomes but by a series or packet of factors. For instance in the fruit-fly, *Drosophila*, at least fifty factors, or 'genes' as they are now usually called, are known to be concerned with the production of eye colour alone. If any one of these is altered the colour of the eye changes, just as though this were controlled by a single gene. The disappearance of the idea of the unit character has greatly influenced not only our ideas about inheritance but has also important bearings on social problems.

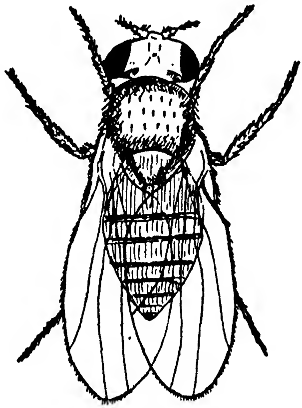


Fig. 39.
The fruit-fly, *Drosophila* (after Morgan).

We may now consider, very briefly, the principal advances that have been made since Mendel founded the science of genetics. The re-discovery of his work in 1900 almost simultaneously by three biologists who had already made considerable advances themselves in that direction, led to a great outburst of work on genetics which shows no signs of abating at the present day.

Pre-eminent amongst modern geneticists stands T. H. Morgan, of America, who has made an intensive investigation of inheritance in the fruit-fly, *Drosophila.*

This animal provides ideal material for genetical investigation, and the immense value of the work done with it is an example of the importance in biology of choosing the right experimental material. *Drosophila* is extremely hardy, can be cultivated with the utmost ease on rotting banana skins, its entire life-history extends but little over a week, while, to crown all, it has only four chromosomes and these are easily distinguishable (see Fig. 40). The advantages are obvious of employing in genetical studies animals in which the generations succeed one another in a smaller number of days than of years in many of the mammals. The knowledge so obtained is universally applicable.

Morgan and his school have done a very remarkable thing. They have actually mapped out the chromosomes. They have determined not only the actual chromosome on which different genes are situated, but the *order* in which the various genes are arranged on the different chromosomes. The small number of the chromosomes in *Drosophila* and their distinctive appearance have been of the greatest help in this. The division of the genes into four groups corresponding to the four pairs of chromosomes has followed from a study of *linkage.* If two characters are controlled by genes situated on the *same* chromosome it is clear that these cannot be inherited independently and that Mendel's second law can only apply to characters produced by genes lying on different chromosomes. The fact that

these linkage groups, or series of characters, which, however the animals are crossed, tend to remain together in future generations, are four in number in *Drosophila*, is, of course, a most potent argument in favour of the chromosome theory of inheritance.

Linkage was discovered by a British zoologist, Doncaster, in 1906, when he found that in the magpie moth, *Abraxas*, the two colour varieties, pale-winged and dark-winged, are definitely linked with the sex of their possessor, the pale variety being almost invariably females. Since that date many similar instances have come to light, probably the most widely known being the association between tortoiseshell colour and femaleness in cats.

These facts indicate that sex is a character on a par with eye colour and so forth and so must be represented by genes lying on particular chromosomes. This brings us to the subject, deferred in the last chapter, of sex determination. We have hitherto spoken of the chromosomes as consisting of two sets equal in numbers and exactly corresponding in appearance. This is literally true of hermaphrodite organisms but is subject to an important qualification in organisms with separate sexes. In many such organisms there have been distinguished either in the male or the female (*never in both*) either one *odd* chromosome or else a pair composed of *unlike* members.

In *Drosophila*, as shown in Fig. 40, there are two large pairs of chromosomes and one small pair, the members of which always correspond to each other, but the fourth pair consists of chromosomes which are

alike in the female but *unlike* in the male. These are the sex chromosomes. The like ones, the two in the female and the one like them in the male, are conventionally known as 'X' chromosomes, and the odd one, where present as in *Drosophila*, as a "Y" chromosome. In some animals, such as birds, it is the female which possesses the unlike pair, the 'X' and the 'Y', and the male the like pair, while in many insects the

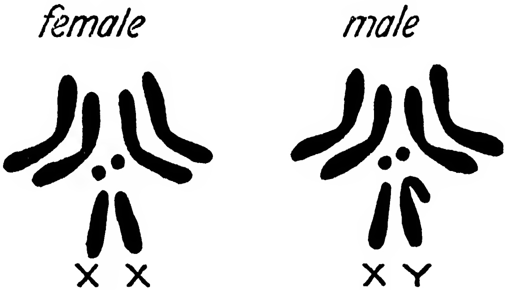


Fig. 40.

Conventional diagram of the chromosomes of *Drosophila* showing the difference between the sets of chromosomes in the two sexes.

female, like that of *Drosophila*, has two 'X' chromosomes while the male has only one, there being no 'Y' chromosome. In this last case the female has therefore an even number of chromosomes and the male, with one less, an odd number.

In this asymmetry of the sex chromosomes lies a very simple mechanism for regulating the approximately equal production of males and females in any species. Let us consider the case of *Drosophila*. The separation of the pairs of chromosomes in the gametes will involve

the formation of only *one* kind of egg, with three ordinary chromosomes or 'autosomes' and one 'X' chromosome, but of *two* kinds of sperms. One of these will have the same chromosomal constitution as the eggs but the other will possess the three autosomes and a 'Y' chromosome. Accordingly one-half of the eggs will be fertilized by the one kind of sperms and the other half by the other. Since the half that are fertilized by the sperms containing the 'X' chromosomes will all contain two 'X' chromosomes they will all develop into females, while the remaining eggs will be fertilized by sperms containing the 'Y' chromosome and so will all become males. A moment's reflection will reveal that any asymmetry in the chromosomes in one or other of the sexes with the consequent production of two kinds of either sperms or eggs will give a similar result.

The influence of the sex chromosomes is best displayed in certain insects which exhibit both male and female characters, a condition known as gynandromorphism. For instance, in a lateral gynandromorph one half of the body is that of a male the other half that of a female. Such animals are always genetically female; in the case of *Drosophila* the zygote has two 'X' chromosomes. The appearance of male characters in certain parts of the body is due to abnormal divisions of the nuclei during development, only one 'X' chromosome passing into daughter nuclei instead of two. These cells and their descendants will, in the absence of the second 'X' chromosome, all exhibit the characters of the male, while if there are any other factors linked to maleness alone these will also appear. The particular

case of the lateral gynandromorph is due to an abnormal division of the nucleus in the actual zygote itself, half the cells of the future body thus possessing two (or more) 'X' chromosomes and the other half one. The absence of the second 'X' chromosome in the male portions can invariably be detected by the usual technique. Many other abnormalities in inheritance have been successfully explained by the discovery that the chromosomal constitution is abnormal. This is probably due to the failure of the chromosomes properly to separate or 'disjoin' (the condition is known to geneticists as non-disjunction) during the maturation of the gametes. For instance a female might produce eggs with either two 'X' chromosomes or with none at all and these when fertilized by the two kinds of sperms would, of course, give rise to no less than four types of zygotes with 'XX', 'XXY', 'X' or 'Y' sex chromosomes, the two first giving rise to females (owing to the presence of two 'X' chromosomes) and the two last to males.

Having described how linkage groups may be identified, we must now describe how Morgan has succeeded in actually working out the order in which the genes lie on the chromosomes. He has done so by a study of what has become known as 'crossing-over'. It has been found by the cytologists that occasionally pairs of chromosomes when they come to lie side by side in the all-important reduction division become twisted. Under these circumstances instead of separating in the normal manner, they break at the position of the twist, the two portions of the different chromosomes

uniting and passing into different cells, the top portion of one, as we may conveniently describe it, attached to the lower portion of the other and vice versa (see Fig. 41). In this way the linkage between two characters may be destroyed.

Now, since crossing-over may occur at any point along the length of the chromosomes it is clear that the farther apart two genes lie on the chromosomes the

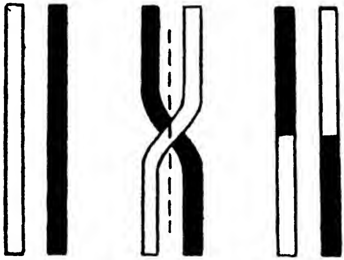


Fig. 41.
Diagram to illustrate 'crossing-over'.

greater the chance of their becoming separated when crossing-over occurs, while the nearer they are together the smaller will be this chance. It has been found that for any two pairs of characters the percentage of recombination is constant and may range for different pairs from 1 per cent to 50 per cent, the genes in the former case being very close and those in the latter being obviously situated at opposite ends of the chromosomes.

It must be clearly understood that the characters produced by the genes under investigation must be

different in the two animals being crossed. For instance when a *Drosophila* with vestigial wings (see Fig. 46) and black colour (an animal which could not survive in nature but which lives well under the artificial conditions of captivity where such individuals turn up from time to time as a result of 'mutations' (see p. 183)), both of them recessive characters carried on the second chromosome (and therefore normally linked), is crossed with a wild individual with the normal dominant, long wings and grey body-colour, the F1 generation all resemble the wild parent. This is to be expected because the characters in which the wild parent differs from its mate are both dominant. The F1 generation is, of course, heterozygous for these characters and produces two kinds of gametes, one in which the second chromosome bears the genes for long wings and grey colour, and the other vestigial wings and black colour. When females of this generation are back-crossed with males with both recessive characters, vestigial and black, we should expect that half of the offspring would also be vestigial and black, the result of the fertilization of the second type of eggs with the one type of sperm produced by the male, and the other half would be like the mother, heterozygous but displaying the dominant characters, long wings and grey colour. Actually, however, only 82 per cent of the offspring are of these two types, the remaining 18 per cent being 'cross-overs', as shown in Fig. 42. Half of these have vestigial wings and grey colour and the other half long wings and black colour. The linkage between vestigial wings and black colour on the one chromosome and between long wings

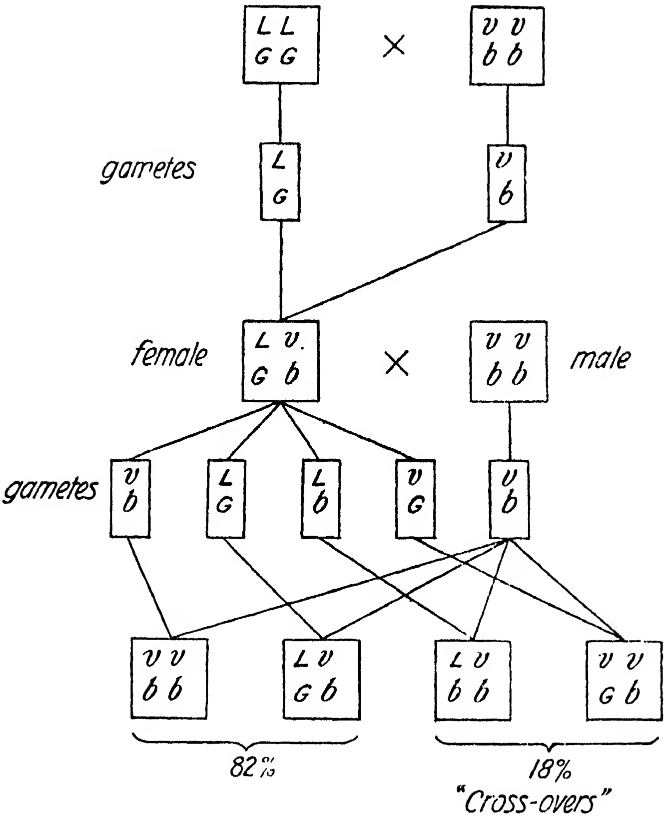


Fig. 42.

Diagram illustrating effect of 'crossing-over' in *Drosophila*, full explanation given in text. *b*, gene for blackness (recessive); *G*, gene for greyness (dominant); *L*, gene for long wings (dominant); *v*, gene for vestigial wings (recessive).

and grey colour on the other has been broken because crossing-over of the chromosomes has taken place in between the positions of the two genes. Great numbers of similar experiments have enabled Morgan and his fellow-workers gradually to construct maps of the four chromosomes of *Drosophila* showing the relative positions on them of between one and two hundred different genes.

Many hundreds of genes must lie on every chromosome and it has been calculated that each is at least as large as the largest organic molecule. But, although they can be assigned a definite position on the chromosomes, it is a mistake to regard them solely as definite structures, however small. They are better considered as centres of chemical activity, producing something akin to enzymes or hormones the results of which are out of all proportion to the amount of substance present. More than five hundred genes in all have been studied in *Drosophila* concerned with such characters as body or eye colour, shape of the body or condition of the wings, the occurence of bristles, and so forth. It is sometimes advanced in criticism of the chromosome theory of heredity that all of these are external characters. This is true, but internal characters cannot usually be studied without destroying the animal and so rendering future breeding experiments impossible.

One type of gene calls for especial mention. There are so-called lethal genes the presence of which prevents the proper development of the organism in which they occur. These have been studied in *Drosophila* where they were originally detected owing to the failure of

certain crosses to produce the expected ratios in the offspring. There is at least one probable case in man, concerned with the condition called brachydactyly which involves a shortening of the fingers and toes. This is dominant so that it appears in an individual heterozygous for it. In every case where the inheritance of this character has been followed, it has been found that the parent possessing it must have been heterozygous because it only appeared in half the offspring, instead of in all of them as must have occurred had the parent been homozygous for this dominant character. It has been suggested with reason that the presence of two genes for brachydactyly is lethal, so that an embryo homozygous for this character must die at or before birth.

Alternative genes affecting the same character, such as those causing long or short stem in peas, are now known as allelomorphs. It has already been noted that Mendel's third law, of unit characters, was based on the assumption that these are controlled by single, alternative factors, but that actually characters may be affected by a great many different genes. The great number affecting eye colour in *Drosophila* is probably unique only because this character has been more intensively studied than any other. As it is we know that a quadruple system of allelomorphs is concerned with coat colour in the mouse. But the classic instance of multiple allelomorphs occurs in the domestic fowl. Four types of combs are possessed by fowls, single, pea, rose and walnut, and genetical analysis has shown that single is probably the most primitive of these, pea or

rose being dominant over it, crosses between either of these and single giving only individuals with the more complex type of comb in the F1 generation. The genes for pea and rose are carried on different chromosomes and when *both* of these are present the fowl always exhibits the still more complex walnut comb which, in turn, is dominant over pea or rose comb.

Although the chromosome theory of heredity *is* still a theory, it is one which explains so many otherwise discordant facts and has formed the basis for so many successful prophecies that it may be regarded almost as established fact. The principle criticism levelled against it is that it endeavours to account for too much ; that all the multitudinous characters of organisms cannot be born on the chromosomes and that some part, and according to some critics the more fundamental part, of the mechanism of inheritance must lie in the cytoplasm. Inheritance through the cytoplasm does apparently occur in some cases, for instance the transmission of the symmetry of the shell in certain fresh-water snails and of the plastids, or progenitors of the chlorophyll granules, in certain plants. Further research will doubtless reveal other instances though whether these will be numerous enough or important enough seriously to affect the general truth of the chromosome theory of heredity is much less certain.

A very great mistake would be made were it assumed, as it might well be after what has been so far said about the mechanism of inheritance, that the characters of the adult organism could be accurately described were all the genes present in the zygote known. It is true

that the organism cannot develop characters for which it does not possess the necessary genes, but at the same time it by no means follows that all the genes present will find expression. The *potentialities* of any organism are expressed by its genetical constitution but the influence of the genes upon the developing organism is modified, sometimes profoundly, by the environment, both outside and inside the organism. Two very useful terms have been coined by geneticists to express these differences. They speak of *genotypes* or groups of organisms with the same genetical constitution and of *phenotypes* which resemble each other irrespective of their genetical constitution. Genotypes may develop into quite different phenotypes if exposed to different environments.

Probably the best examples of the influence of environment on the modification of genotypes are concerned with the expression of sex. We have seen how sex is determined by the chromosomes, that is by the genetical constitution. Apart from hermaphrodites, organisms are either genetically male or genetically female. In the great majority of cases they develop into males or females respectively, but there are certain exceptions which are of the greatest interest. There is a certain worm-like creature called *Bonellia* which lives in the sea and has a rounded body some two inches long and a lengthy, very extensile proboscis. All of these individuals are female, the males consisting of minute, semi-transparent creatures which live parasitically in the kidney sacs. All the very young *Bonellia* are alike and their eventual fate depends on the environment in

which they develop, if they settle on the proboscis of a female they develop into males, but if they settle down to a free existence they as certainly become females. There is also the case of a limpet called *Crepidula* which lives in chains, one individual being attached to the shell of the animal beneath it. The oldest members of any chain are always female, the middle ones hermaphrodite and the youngest male. If a young *Crepidula* attaches itself to the end of a chain it becomes male, later hermaphrodite and finally female, but if it settles down by itself to form the beginning of a new chain it develops directly into a female.

Such cases are explicable on the assumption, for which there is considerable evidence, that every organism has potentially the power of becoming either a male or a female, the male possessing an excess of 'male-producing substance' over 'female-producing substance' in the sex chromosomes, the reverse being the case in the female. If any animal during development comes under the influence of conditions which alter its rate of growth and its usual internal co-ordination the sex-producing substance, hormone or whatever it may be, which would normally be suppressed may be able to assert its influence and so an animal genetically of one sex may actually develop into the opposite sex.

Yet clearly genotypes are more likely to develop into similar phenotypes than are other individuals. The best example of this is provided by the study of identical or 'like' twins. As is well known there are two kinds of twins: those which have no more resemblance

to each other than any other children of the same parents and which may be the same or of different sexes and are known as unlike twins, and others which resemble each other very closely and are *always* of the same sex. It is generally agreed that the former are due to the simultaneous fertilization and development of two eggs while the latter are the result of the separation of the first two cells of the same developing zygote and of the subsequent independent development of these. Like twins have therefore the same genetical constitution and are in a real sense the same individual since they have developed from the same zygote. When such twins are brought up together, exposed to the same environment, their resemblance not only in appearance but also in character and intelligence is striking in the extreme. Even when they have been separated at an early age (and a number of such cases have been carefully studied) and have been brought up under very different conditions, not only do they still resemble each other greatly in appearance when adult, but they are also much more alike in intelligence than are any average pair of brothers or sisters. They may, it appears, vary much more emotionally than intellectually under such conditions, intelligence being more rigidly determined by genetical constitution while behaviour and what is known generally as character are determined to a much larger extent by environment and training.

Mendelian inheritance is of universal application to all organisms, plants and animals alike, which possess organized nuclei. Mendel's original experimental material consisted of peas, Morgan has built up the

great edifice of the chromosome theory of heredity after breeding untold generations of fruit-flies, primulas are used for the most intensive work on genetics now being carried on in this country, while the genetics of farm crops and domestic animals, such as wheat and poultry or cattle, are everywhere being exhaustively studied.

The general principles of inheritance derived from the study of these different plants and animals apply with equal force to man. The inheritance of brachydactyly and the characteristics of like twins have already been touched upon, but these are only two instances out of many. Albinos appear from time to time amongst men as they do in many groups of animals, this condition, due to an absence of pigment, is a recessive character and only appears, therefore, when two individuals, both heterozygous for it, chance to mate. Eye colour is also inherited in the same manner, brown being a dominant and blue a recessive character. Sex-linked characters are well known, notably colour-blindness, night blindness and haemophilia. The last-named is a serious condition, for it consists of an enzyme deficiency in the blood which makes coagulation impossible so that it becomes extremely difficult to stop the flow of blood from even the smallest wound. It only occurs in the male sex but is carried by the female sex, always skipping a generation.

Certain other definitely pathological conditions are known to be produced by genes because they are inherited according to Mendelian laws and this may be true for certain types of feeblemindedness. Nevertheless those apostles of eugenics who would institute a

rigorous control of human mating, or rather human reproduction, are pressing for something which is not only very difficult to carry out in practice, but is also of very dubious value biologically. The best that can be hoped for from eugenics (at any rate for a long time to come) is the cutting out of definitely harmful characters which are known to be controlled by genes. For the rest the mating of brilliant parents, though it may produce on the average rather more intelligent children than the mating of stupid parents (and such apparent differences may be due in part to the differences in environment) is just as unlikely to give rise to children of exceptional brilliance. The eugenicists overlook environment which *can* be controlled and, for the great majority of the population, vastly improved. We can so order social conditions that the highest qualities which are latent in the genetical constitution of any child shall find expression in the characters of the man or woman into which it will develop. The genes on the chromosomes cannot be altered but they can be so influenced as to produce the best possible results. In the words of Aristotle, paraphrased by Jennings,[1] " the inheritance of man is not alone what he is born with, but what he can develop ".

[1] See *Prometheus or Biology and the Advancement of Man*, by H. S. Jennings, an admirably succinct account of the social applications of genetics.

CHAPTER III

THE ORGANISM AS A WHOLE

In the various sections of the preceding chapter of this book attention has been confined primarily to an analysis of living organisms. These have been separated into their constituent parts and the structure of these and their mode of functioning briefly described. Investigations of this character are essential to the right understanding of living matter, but they do not tell us everything about the organism. The physiologist and the bio-chemist remove muscles and nerves or obtain enzymes from the digestive juices or hormones from extracts of the ductless glands and then study in the greatest detail the nature and properties of these. This analysis is the essence of the scientific method but, at any rate as yet, we are unable from its results fully to understand the organism.

There are certain aspects of living matter which in our present state of knowledge can certainly only be described in terms of the whole organism. It is with these that this section is concerned. We have already seen how the essential instability of living matter lies at the basis of muscular and nervous activity, of metabolism, and indeed of all the characteristic properties of life. We must now consider the effects of this instability on the organism as a whole.

1 Adaptation

Living matter has come to assume innumerable forms which range through every conceivable environment. Organisms exist in water, on land and in the air; they are found at the poles and at the equator, in the surface waters, the mid-depths and the abyssal regions of the oceans, in rivers and in subterranean caverns, on mountain tops and in deep valleys, in tropical rain forests and in the most arid deserts. Adaptation is the name given to the property which has enabled living things to maintain themselves under these widely diverse conditions. Indeed adaptation has been described as *the* fundamental property of life, and in so far as it is an expression of the essential instability of living matter there is an element of truth in this description.

Adaptation is a matter of function. It is, in its essence, the capacity which all plants and animals must possess—or they could not exist—of maintaining their individuality in the face of the antagonistic forces of the physical environment, represented by such factors as extremes of temperature, lack of water or of oxygen, and so forth. Those regulative processes which control the temperature of an animal or its rate of respiration are examples of adaptations which have enabled life to exist under continually changing conditions.

But the term adaptation has in the past been associated particularly with changes which have enabled organisms, either by conquering new environments to establish themselves under new conditions,

or else have rendered them better fitted than their fellows for life in the same environment as before. Especial stress has been laid on obvious outward changes in the structure or appearance of the organism, the classic instances of adaptations having to do with protective coloration, mimicry or warning coloration. While there is no doubt that too much has frequently been made of these, those who have had experience of living animals in nature find it difficult to question the reality of at any rate the more extreme instances of such adaptations. There is an Indian insect, called *Phyllium*, frequently displayed in museums, the resemblance of which to a leaf is startling in its exactness; in colour, shape, even to venation and the blotchings due to fungus attack. Seen alive the resemblance is still greater, for the insect perpetually sways to and fro as though blown, like a leaf, by the wind. There is a type of calcareous marine weed, *Halimeda*, common in coral reef seas which is composed of somewhat irregular lobes united by fine connections. On this weed lives a small crab called *Huenia*, which has precisely the same outline, flattened shape and vivid green colour as the lobes of *Halimeda*. It is, unless actively sought for, absolutely indetectable when attached to the weed. As far as their detection by the eye of man is concerned, both of these animals are unquestionably ideally protected. But of course in neither case is man the enemy. The true 'protective' value of their colour and shape must be estimated in terms of the sense organs of their enemies. If these perceive their prey by smell (or 'taste' from a distance in the case of marine animals)

then 'protective' colour is useless, if they hunt by the aid of eyes like our own then these animals probably are protected to a large extent by their extreme resemblance to their surroundings. Unfortunately it is very difficult to analyse the receptive powers of an animal, though the study of conditioned reflexes has put a weapon in our hands which may prove of the greatest assistance in the future. But not until such analyses have been carried out can the case for protective resemblance and allied instances of 'adaptations' be either proved or disproved.

Examples of adaptations frequently cited are concerned with organisms which depart in some rather startling way from the general type of other species in the same group, the result, unquestionably, of adaptation to some peculiar mode of life.

Thus we associate mammals with life on land, they certainly sprang from land animals and evolved the characteristics peculiar to them (notably hair, viviparity and the production of milk) on land, where the majority of them are still to be found. But in the course of evolution certain groups of mammals betook themselves to new surroundings. Several groups, independently of each other, took to the sea and one of these gave rise to the cetaceans, which include the whales, dolphins and porpoises. These animals are admirably adapted for life in water: their bodies streamlined like those of fish; their fore-limbs modified to form paddles; their hind-limbs reduced to the smallest vestiges; the necessary insulation supplied by subcutaneous layers of blubber. Another group of mammals, which includes

the bats, acquired the power of flight, the greatly elongated digits supporting the membraneous wing. At the same time other mammals became highly specialized for particular modes of terrestrial life, such as the horse, the limbs of which constitute one of the most perfect mechanisms for rapid movement over the surface of the earth. To attain this degree of perfection all the digits save one have effectively been lost and the horse literally runs on the tips of single fingers and toes, the nail being represented by the hoof. To outward appearance few organs could be more dissimilar than the flippers of whales, the wings of bats and the limbs of horses, yet all are but modifications of the same pentadactyl limb of the mammals, the result of adaptations to different modes of life.

Examples such as these certainly emphasize very forcibly the fact of adaptation but they lay too much stress on the structural aspect which is but the outward and visible manifestation of more fundamental functional changes. We may indeed distinguish between structural, or morphological, and functional, or physiological, adaptations and such a distinction is useful so long as it is realized that the two are, at bottom, the same.

No better instance of adaptation, embodying examples of both structural and functional changes, can be found than that supplied by the shipworms (*Teredinidae*). These are bivalve molluscs which spend their post-larval lives burrowing into timber in the sea. The damage they did to the vessels of the early mariners brought these animals speedily to the attention of

mankind, by whom, on account of their naked, elongated bodies, they were for a long time classified as worms.

A comparison between the structure of a typical bivalve, such as the clam shown in Fig. 2, and that of a shipworm at once reveals the essential similarity between the two and at the same time throws into relief the adaptations which have fitted the latter for its peculiar mode of life. To begin with the shell: this in

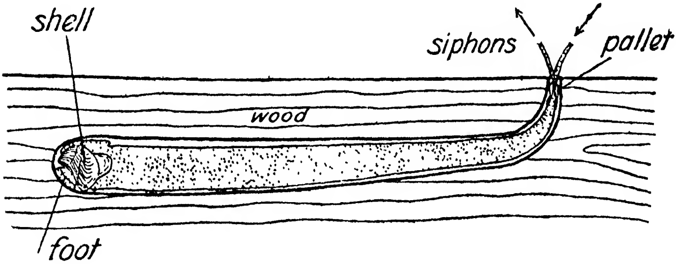


Fig. 43.
Appearance of the shipworm, *Teredo navalis*, in burrow in wood.

the clam, as in the great majority of bivalves, covers the entire body and serves for protection and for the support of the body. In the shipworm, as shown in Fig. 43, it is confined to the extreme front end of the animal. It is no longer needed for either protection or support, for the animal lives encased in a narrow burrow. But it is not retained as a mere useless vestige, it is the most important organ in the body of the shipworm, without which existence is impossible. It forms the cutting organ and is most beautifully adapted for this function.

The two valves (Fig. 44) are divided into three portions: a hind, wing-like lobe called the auricle, a median semi-circular lobe which forms the bulk of the shell and a triangular anterior lobe which extends for about half the breadth of the median lobe. The outer

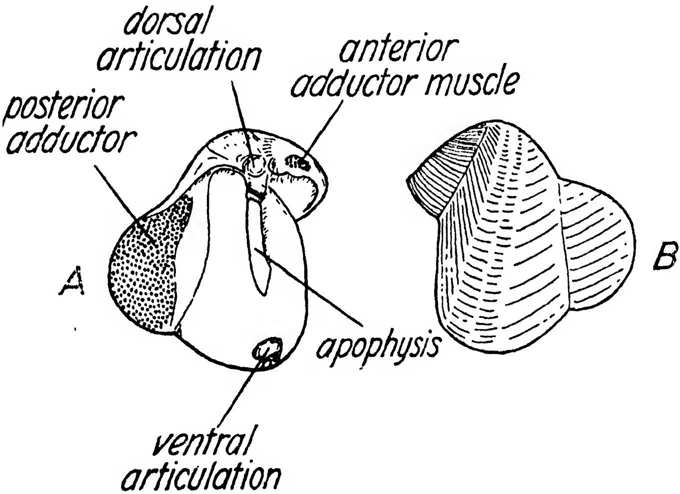


Fig. 44.

Inner (*A*) and outer (*B*) aspects of shell of *Teredo navalis* (modified after Miller).

surfaces of the median and anterior lobes are covered with a series of sharp ridges, those on the former extending diagonally across the anterior third of its surface while those on the latter run parallel to the sharply cut away lower margin. These ridges are continually being added to during the life of the animal. On the inner side of the median lobes are two rounded

projections, one above and one below, by means of which the shell valves are articulated. This double articulation is an adaptation peculiar to the shells of the shipworms, in other bivalves there is only the single hinge, on the upper or dorsal side.

In all the bivalves the shell valves are connected by transverse bands of muscles called adductors, the contractions of which draw the valves together and so cause the shell to close. After a bivalve dies the shell valves always gape because the muscles can no longer contract and the elastic ligament at the hinge causes the valves to spring apart. There are usually two adductors, one posterior and one anterior, as shown in Fig. 2. In the shipworms these two adductors are present (Fig. 44), but they have new functions. There is a very large posterior adductor attached to the inner sides of the auricles and a much smaller anterior one which extends between the inner sides of the anterior lobe. By the alternate contractions and relaxations of these two muscles the shell valves are rocked to and fro on the two articulations, the edges of the valves describing an arc of between 20 and 30 degrees.

Yet another organ is concerned with the mechanism of boring. At the front end of the animal and rather on the under side, in the space left uncovered by the shell owing to the abrupt termination of the anterior lobes, there is a round, fleshy structure which acts as a sucker. This is the foot, an organ which in other bivalves is usually long and wedge-shaped and is concerned with locomotion, a succession of convulsive movements enabling its possessor to proceed through

sand or mud by a series of hops. In the shipworms the foot has a very different function. It grips the wood at the end of the burrow and so enables the shell valves to bear against the wood and, by their boring action, extend the burrow. It is essential that the foot should grip the wood very firmly and this necessitates powerful muscles which, in turn, must have a firm attachment on which to contract. This attachment is provided by a pair of long processes of the shell, known as apophyses, which extend downwards from the upper articulations. These structures are present only in shipworms and in a few allied stone borers.

We are now in a position to describe the process of boring. Attachment is given by the foot below, assisted by a flap of skin which overlaps the shell valves above (see Fig. 43), and the shell is pressed firmly against the wood. The powerful posterior muscles are contracted, thereby drawing the auricles together and forcing the anterior lobes apart. The sharp ridges upon these scrape away the wood at the end of the burrow while the ridges on the median lobes widen the opening behind. The posterior muscle then relaxes and the anterior one contracts, drawing the anterior lobes together. This is a much easier operation because the wood offers no resistance to movement in this direction, which explains the much smaller size of the anterior muscle. After each movement of the shell valves the foot loosens its grip and moves a short distance to one side, after which another scraping movement is carried out. This goes on until the shell and front half of the animal have become twisted through 180 degrees when the foot

reverses its movement. In this way a smooth and perfectly circular burrow is cut.

The whole process of boring is a model of efficiency. Yet, as we have seen, it is executed by a cutting organ which is a modification of the purely protective shell of other bivalves, by muscles which are equivalent to those which normally close the shell, and by a sucker which is actually the modified organ of locomotion in other bivalves. The only new structures are the lower articulation of the shell valves and the apophyses to which the muscles of the foot are attached.

But the elongation of the body and the presence of a boring mechanism are not the only modifications which have enabled the shipworms to exist in burrows excavated in wood. They actually obtain nourishment from the wood into which they bore. All the fragments scraped off by the shell are passed into the mouth which lies just above the foot and pass through the alimentary canal before being passed to the exterior. Within the alimentary canal there is a large extension of the stomach, not present in other bivalves, where these fragments are stored. There is also a special region surrounding the stomach where these fragments, and nothing else, are ingested intracellularly. This region also is present only in the shipworms. A digestive enzyme is elaborated in this region which can break down the complex carbohydrate, cellulose, which forms a major constituent of wood, into glucose. The power of digesting cellulose is extremely rare in the animal kingdom, being confined, in the molluscs, to a few

herbivorous snails amongst the univalves and to the shipworms alone amongst the bivalves.

The last adaptation we have to consider concerns the closing of the burrow. Shipworms frequently bore into wood, such as the strut roots of mangrove trees in the tropics or pier piles in all parts of the world, which are uncovered by the sea at low tide. This necessitates some effective means of closing the burrows and so preventing drying up. Normally two fine tubes called siphons project from the fine opening of the burrow (the animal enters when very small and then enlarges the burrow inside as it grows). Through one of these water with finely divided food is drawn in, oxygen being obtained from the water and protein and other constituents not present in wood from the food. Through the other water and waste matter, including the wood which has passed through the alimentary canal, are ejected. These siphons can be withdrawn when necessary and at the same time a pair of club-shaped plates, formed, like the shell, of limy material, and which are attached to opposite sides of the body at the base of the siphons, are forced forward, completely blocking the opening. These pallets, as they are called, are found only in the shipworms.

The modifications which have fitted the shipworms for their characteristic mode of life include, therefore, morphological adaptations such as shape and character of the shell and the foot and the enlargement of the stomach and the presence of the special region for the digestion of wood, and also physiological adaptations such as the acquisition of an enzyme capable of digesting

cellulose. All of these, including possibly the enzyme, represent the modification of previously existing structures or substances, exceptions being the second articulation of the shell, the apophyses and the pallets. This draws attention to a fact of fundamental importance. Animals wherever possible adapt old structures to new uses and even when they have taken to an entirely new mode of life seldom produce entirely new structures. The examples furnished by the shipworms are but a few out of very many. The thyroid gland of the vertebrates arises from an organ which in the more primitive members of that group produces the mucus needed to entangle food collected by ciliary currents. Two of the three ear ossicles in the mammals almost certainly represent bones found in the angles of the jaw in the lower vertebrates such as the reptiles. The skeleton of the tongue and of the voice box in the higher, air-breathing vetebrates, is derived from portions of the supporting skeleton of the gills in the fishes.

The study of adaptations reveals that though animals are extraordinarily plastic, alike in structure and function, yet they never depart from the fundamental ground plan of the particular group to which they belong. Whales, bats and horses are all in the first place mammals and only in the second place adapted for life in water, in the air or on land. Leaf insects and shipworms however atypical they appear at first sight are clearly revealed after detailed examination as insect and bivalve mollusc respectively. Even the internal parasites, more modified though they be than

any free-living animals, exhibit their affinities clearly enough when their development is studied. The true nature of any organism is revealed, therefore, not by what it is but by what it sprang from, a fact which leads us logically to the consideration of evolution which forms the subject matter of the succeeding sections.

2 Evolution

It is the especial distinction of Charles Darwin that he forced belief in evolution upon an unwilling world. He did so in the first place by a consumate marshalling of the diverse but irresistible evidence in its favour, and in the second place by the elaboration of the theory of Natural Selection which he put forward as the possible explanation of the evolutionary process. It is in his former, and probably greater, capacity that we are concerned with him in this section.

Evolution is a fact. Theories of evolution are concerned with the way in which it came about ; their multiplicity is evidence not of any lack of belief in evolution but on the contrary of universal conviction amongst biologists of the fact of evolution which these theories seek to explain. Many biologists reject Darwin's theory of Natural Selection or consider it to be no more than a partial explanation of the facts, but none of them question the occurrence of evolution which was established for all time in *The Origin of Species*.

But although we are quite certain that evolution has taken place and that it continues to operate, we cannot as yet prove it. For the past two thousand

five hundred years, beginning with the early Greeks, man has been accumulating facts about biology, with ever-increasing acceleration during the past century and a half. The only great generalization which has emerged from this mass of information is evolution. The facts of comparative anatomy, of embryology, of systematics, of palæontology or the study of fossils, and of geographical distribution, are all of them explicable on the assumption that evolution has taken place. No other explanation even remotely fits these innumerable facts or is for a moment credible in the light of them all.

Darwin with the broadly-sweeping and discerning eye of genius surveyed all of these facts and drew the only possible conclusion from them. But these facts had been accumulating for long centuries and the idea of evolution was itself far from new when Darwin published *The Origin of Species*. It had been held by many biologists and thinkers from the time of the Greeks onwards but those who held it were unable, as Darwin finally did, to convince mankind at large of the truth of their views. Biological knowledge had to progress beyond a certain point before this became possible.

Above all it had to be universally realized that animals always spring from similar animals, that like begets like. This seems obvious to us now but belief in the spontaneous generation of living from non-living matter only died within very recent times. Aristotle thought that the majority of the simpler animals arose in this way and that even mice were generated in putrifying matter. Virgil in his *Georgics* gives a

well-known account of how a swarm of bees (actually drone flies) may be produced from the decaying body of an ox. All manner of animals—worms, insects, snails and eels amongst them—were universally believed to arise by a process of spontaneous generation from mud, dung and putrifying matter of every description.

Not only was it believed that living matter might arise spontaneously from non-living matter but the view that one type of living matter might originate from another was widely held. The most famous instance of such beliefs is the myth of the barnacle geese.[1] These birds it was stated arose from stalked barnacles which grew on trees. An immense literature grew up on this subject culminating as late as 1677 in a paper published in the *Philosophical Transactions of the Royal Society of London* by its first President, Sir Robert Moray. In this he described in the most minute detail how every part of the bird appeared in miniature within the shell of the barnacles, " The little Bill, like that of a Goose; the Eyes marked; the Head, Neck, Breast, Wings, Tail, and Feet formed, the Feathers everywhere perfectly shaped and blackish coloured; and the Feet like those of other Water-foul, to my best remembrance."

Such opinions died hard. The Italians Redi (1621-97) and Spallanzani (1729-99) were the first to subject them to experimental test and played a leading part

[1] See *Barnacles in Nature and in Myth* by E. Heron-Allen, for a fully documented and delightfully written account of this belief.

in their destruction so far as the multicellular animals were concerned, but it was left to Pasteur in the latter half of the nineteenth century to prove, again in the teeth of bitter opposition, that unicellular organisms, including bacteria, never arise by spontaneous generation. The final establishment of the continuity of living matter, or of the Principle of Biogenesis, by demonstrating that all organisms have sprung from pre-existing organisms, cleared the way for the similar establishment of the fact of evolution.

Evolution involves the conception that all organisms have sprung from different, and probably simpler, ancestors and that all the interrelations between organisms and between these and the physical environment have similarly arisen from different pre-existing conditions. The alternative view, almost universally held until the middle of the last century, was that all organisms had been especially created in the first place, although some believers in special creation were willing to admit that some slight modifications of the original type might have occurred during the passage of time. But they were far from believing, as do modern biologists, that even the most widely diverse forms of animal or plant life had a common origin in sufficiently remote time.

Those who believed in the fixity of species thought of organisms always in terms of what they were and what they did; they thought of them as being created with a definite purpose. We who believe in evolution, on the other hand, consider organisms always in terms of what they sprang from, their origin not their

end, a conclusion to which the consideration of adaptation led us in the preceding section.

Aristotle, the first of the great biologists and not without claims to being the greatest of them all, believed in the fixity of species but he nevertheless laid, and laid truly, one of the corner stones of the edifice of evolution. The comparative study of the structure of animals led him to the conception of the Community of Plan, or Unity of Type as it is sometimes called. He found, for instance, that whales, dolphins and porpoises which live in the sea and both look and behave in many respects like fishes, actually breathe air and are viviparous and belong to the group now known as the mammalia. He also noted that even animals apparently so dissimilar as man and fishes have many structures in common, such as the backbone, the principal blood vessels, the liver, spleen, kidneys and so forth. He was able, owing to their possession of this common ground plan, to separate the vertebrates, to which both of these types of animals belong, from the other great groups of the animal kingdom.

He succeeded in this way in delimiting one of the great groups of animals which we now call phyla, each of which consists of a number of animals which, however diverse they may appear at first sight, are characterized by a fundamental community of plan. Had animals come into existence in the first place fully adapted to the particular mode of life they now possess, there is clearly far greater likelihood of flying animals, such as bats, flying fish or insects, of swimming animals, such as whales, herrings, squids and lobsters, or of

terrestrial animals, such as hares, climbing perch, centipedes or snails, resembling each other closely than of their resembling animals with quite different habits. Actually the reverse is the case. The flying bats, the swimming whales and the terrestrial hares are all structurally akin, all are included within the class mammalia of the phylum vertebrata. The flying fish, the swimming herring and the climbing perch, are as structurally alike as they are diverse in habit, they also are members of the phylum vertebrata but in the class pisces, related to but essentially simpler than the class mammalia. The flying insects, the swimming lobster and the terrestrial centipedes are all of them members of a different phylum, the arthropoda (jointed-limbed), while the swimming squids and the terrestrial snails belong to yet another phylum, the mollusca, these phyla being as different in ground plan from each other as they are both from the vertebrates.

It took man many centuries before he understood enough about comparative anatomy adequately to classify the animal kingdom. When this was accomplished, in broad outline at any rate, the only satisfactory explanation of the infinite diversity of habit and superficial structure amongst members of the various phyla, some twenty of which have been definitely established, was that furnished by evolution.

This conclusion was driven home with increased force by evidence from two other aspects of the study of structure, from a study of embryology and of palæontology, of the development or history of the individual and of the history of the race.

What, when we come to consider the matter, is the development of an individual from an egg consisting of a single cell to a fully-grown adult composed of many millions of cells constituting the most diverse tissues and organs, but a form of evolution? Development involves the gradual change of the simple into the more complex. Now it is universally true that the early developmental stages of different organisms resemble each other much more closely than do the adults. The freely-swimming larvæ of the oyster resemble not only those of the other bivalves, such as mussels, cockles and also shipworms, but also those of the marine snails or univalves which are also molluscs, it is true, but members of a different class, while the earliest larvæ of both bear a striking resemblance to those of the marine worms which belong to a different phylum altogether.

The early embryos of the mammals, birds and reptiles not only resemble each other very closely but they actually possess at one stage in their development many of the structures we associate with a much more simply constituted class of the vertebrates, namely the fishes. The sides of the neck are pierced with gill-slits, the blood circulates in a series of aortic arches around these, and the axial skeleton consists of a notochord which is first divided into cartilaginous blocks, as in the adult skates and dogfish, before it is finally transformed into bony vertebræ.

For many centuries the barnacles were classified with the bivalve molluscs because, like these, the body of the adult is enclosed in a limy shell. But when

eventually their development came to be studied it was found that they all pass through an early free-swimming stage, the structure of the larva being that of a typical crustacean. Certain of the barnacles have taken to a parasitic existence, notably one called *Sacculina* which lives within the body of crabs. The adult consists of no more than a bag containing the reproductive products which projects from the under side of the abdomen of the crab, with a series of fine branches which ramify through the body of the crab and so obtain nourishment. Yet here again a study of embryology reveals that *Sacculina* is a crustacean and belongs to the same group as the barnacles because the free-swimming larvæ are more like those of the barnacles than of any other group of crustaceans.

During the past century when the facts of embryology were rapidly being discovered, certain zoologists were so impressed by these recapitulations of ancestral history in the development of the individual that they spoke of an animal, in its development, "climbing up its own genealogical tree". Though this is somewhat of an exaggeration—for the embryo of a mammal, for instance, resembles only the embryo of a fish, never an adult fish; though gill-slits do appear functional gills never grow out from these—yet it contains an element of truth. The resemblances between the embryos of mammals, fishes and all other vertebrates, between the larvæ of molluscs and worms, and between those of barnacles, including *Sacculina*, and of more typical crustaceans, can all of them *only* be satisfactorily explained on the assumption that evolution has taken place.

Here again the facts of embryology had to be obtained before this line of evidence in favour of evolution was available. This was a particularly long and difficult process which could only be completed after the invention, about the beginning of the seventeenth century, of the compound microscope and its subsequent elaboration. For many years embryology was the centre of a great controversy. Some biologists believed that in the development of the organism general characters appeared first and special characters later. This process of emergence was known as epigenesis, it was first put forward by Aristotle and subsequent research has proved him, as in so much else, to have been correct. The opposing school of thought believed in preformation, that is in the presence, in miniature, within the egg (or spermatozoon) of all the organs of the adult. Development involved no more than an increase in size of organs already differentiated. This belief was in its very nature absurd since it involved, as its opponents were quick to point out, the presence of untold generations within progressively smaller limits, within the body of every animal. Eve, it was estimated, must have contained within herself the preformed embryos of no less than two hundred millions of human beings. Belief in preformation persisted for a considerable time in a less crude form and so long as it did so it constituted an effective barrier to belief in evolution.

The study of the history of the races of animals and plants as revealed in fossil records is of still more recent development. Certain of the Greeks hazarded

the opinion that fossils were the remains of organisms which had once existed, while Leonardo da Vinci, supreme in science as in art, maintained that fossils found in mountains had been deposited there in past time when this land now raised high above the surface of the sea had been beneath it. The Dane, Niels Stensen (1669) held similar views and gradually the opinion gained ground that fossils were the remains of animals and plants and had not been formed, as formerly believed, by a mysterious plastic power in the earth. But the claims of Hebrew mythology had to be satisfied and fossils were accordingly regarded as the remains of organisms which had been deposited on the surface of the land during the time of the flood. The fossilized remains of a large salamander found in Switzerland were described as those of a child overwhelmed by the deluge!

The great French zoologist, Cuvier (1769-1832), by his classic researches into the fossil remains of extinct animals was the first to demonstrate that no study of animal form is complete which fails to consider the past as well as the present. About the same time the science of geology began to make rapid strides, largely through the work of two British workers, Hutton (1726-97) and William Smith (1769-1839) who, in the Principle of Uniformity, established the conception that the crust of the earth is covered with a succession of strata, laid down originally under water, each characterized by a definite collection of fossils. From this time the science of palæontology, the connecting link between zoology and geology, made rapid

strides, until to-day it provides a great body of knowledge as to the past history of the animal and plant kingdoms, knowledge which is continually being increased as fresh discoveries are made.

The evidence in support of evolution supplied by palæontology is of the first importance and this despite the fact that only remains of those animals which possessed hard skeletons have been preserved with, of course, little or no evidence as to the nature of the soft parts. In the earliest sedimentary rocks all of the great invertebrate phyla are represented. In some cases the fossils probably represent ancestors of forms now living, in others they consist of representatives of groups now extinct, such as the trilobites allied to the modern crustacea, the graptolites possibly similarly related to the hydroids, and several groups of echinoderms. In yet other instances the fossils, even in the very earliest deposits, do not differ essentially from animals now living, notable cases being those of the brachiopod or 'lamp-shell', *Lingula*, of the limpet, *Patella*, and of the bivalve, *Nucula*.

But one phylum, which the study of comparative anatomy has revealed as the most highly organized and most recently evolved, namely the vertebrata, is unrepresented in the earliest fossil-bearing rocks. This great group has originated and then evolved from fish, through amphibians and reptiles, to mammals and birds, during the long but finite period of time which has elapsed since the first sedimentary rocks were laid down. It is indeed fortunate that the skeleton is one of the most characteristic features of the vertebrates

as a whole and also of the great classes into which the phylum is divided.

The classes of the vertebrates appear in definite sequence in the ascending strata. The fish first appear in the Silurian (see Fig. 45) probably reaching their maximum in the Lower Carboniferous. At this period the first land vertebrates, the amphibia, made their appearance, successfully established themselves and, as the dominant constituents of the land fauna, increased greatly during the Upper Carboniferous and Permian periods. From them sprang the reptiles, the first vertebrates completely to emancipate themselves from dependence on water, for all amphibians must, like the frog tadpole, spend at least the early part of their lives in water. The less efficient amphibians shrank in numbers as the reptiles increased, for these creatures, already well established in Permian times, became masters of the earth for the vast period of time during which the Triassic, Jurassic and Cretaceous strata were laid down. They evolved in every possible direction, immense dinosaurs, the largest creatures which have ever existed on land, held dominion over the surface of the earth, flying pterodactyls were masters of the air, ichthyosaurs and plesiosaurs ruled the sea. Nothing, it must have appeared, could ever dispossess these powerful and ferocious animals.

But in time, like the amphibians before them, the reptiles shrank in numbers and to-day only the snakes, crocodiles, lizards and tortoises remain out of the once vast assemblage. In their place arose the mammals and the birds. Both of these arose from primitive

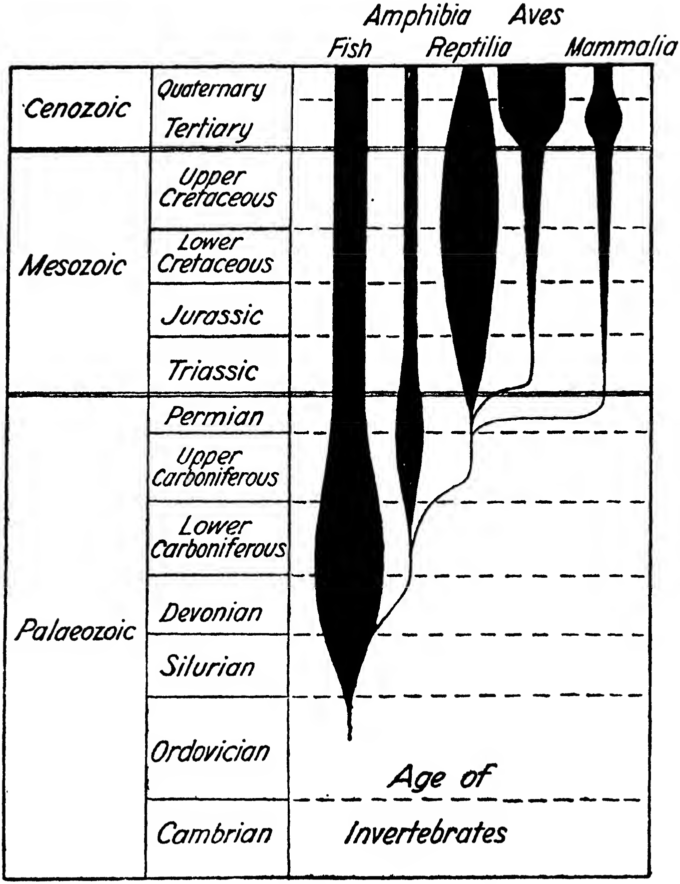


Fig. 45.

Diagram showing the successive appearance of the five great classes of the vertebrates in geological time (modified after Newman).

reptiles of different types, the mammals about the end of the Triassic and the birds at the beginning of the Jurassic. The line of descent of the mammals can be traced in quite remarkable detail from the unspecialized theromorph reptiles, that of the birds is less clearly indicated in fossils so far discovered but there are some very interesting intermediate forms with the feathers and other essential features of a bird yet with the teeth, clawed digits and long tail of a reptile.

The birds have been, as a group, the most successful of all the vertebrates. Comparatively few forms have become extinct whereas the mammals, apparently as successful and certainly with greater powers of adaptation, were formerly represented by many more species than they are at the present day. The marsupials, once widespread, are now practically confined to Australia, where alone they do not have to face competition from the more efficient higher mammals or placentalia, the giant ground sloths of South America are now extinct and so are the mammoths, the sabre-toothed tigers and the Irish elk. And these are only a few of the failures amongst the mammals.

The fish, though there are many extinct species, consisting largely of early 'experimental' forms, have maintained themselves as the dominant group in the sea for life in which they are so admirably adapted. The birds are equally supreme in the air and the mammals, despite the tenacity with which the remnants of the reptiles maintain themselves, the land. They have also, in the form of bats, invaded the air and, with much greater success, the sea, where the

whales, dolphins and porpoises are so perfectly at home that they even breed in the water which the still semi-terrestrial seals and sea lions are unable to do.

The most remarkable thing about the geological record, despite its innumerable gaps, is its completeness. For it must be remembered that, particularly amongst land animals, only very rarely would they die under conditions and in surroundings which would ensure the preservation, in fossil form, of their skeletons. Moreover only a very small portion indeed of the strata which cover the surface of the earth have been uncovered, by faulting, erosion or by the action of man in the excavation of quarries, mines and cuttings, so that only a minute proportion of the fossils present can have been unearthed and examined. Yet even as it is we possess extraordinarily exact records of the ancestory of certain animals. Thus no fewer than 260 extinct species of ungulates are known which are either ancestors of the modern horse and its relatives or were closely allied to these ancestors. We can trace out the development of the horse from a small creature with five digits, a short skull and with a normal dentition, to the present representatives, the most perfectly adapted of all mammals for speedy movement over hard ground, with a single functional digit, an elongated skull and a reduced dentition highly specialized for the cropping and chewing of grass. With such records available after so small a portion of the sedimentary rocks have been examined, how much more may not yet be known about the history of the race ?

The geographical distribution of animals provides further evidence in favour of evolution. This side of the evidence has a particular interest because it was the consideration of these facts which first drove Darwin to the intensive study of evolution which resulted, after twenty-two years of patient work, in the publication of *The Origin of Species*. The opening sentence of that book may suitably be recalled, "When on board H.M.S. *Beagle*, as naturalist, I was much struck with certain facts in the distribution of the organic beings inhabiting South America, and in the geological relations of the present to the past inhabitants of that continent."

If evolution has occurred then we should expect certain evidence of this in the present distribution of animals and plants. In land masses now widely separated from each other the populations should be distinct from one another, the older any group of organisms the more wide-spread it should be and conversely the more recent the more restricted, finally if individuals of the same species have become separated from each other they should tend, as time passes, to diverge. Now this is exactly what does occur. The faunas of, for instance, tropical South America, Central Africa and the East Indies, though living under very similar conditions are quite distinct, more so in the case of South America than in the other two. The fauna of Australia, a land mass long separated from the other continents, is unique, the mammal population consisting of monotremes and marsupials now practically extinct elsewhere. The lung fishes, a very archaic

group which fossil records reveal once to have been very abundant, but which are now restricted to three species, have a very wide distribution. One species lives in Central Africa, one in South America and one in North-eastern Australia. The still older *Peripatus* (not unlike a caterpillar and a very interesting link between segmented worms and crustaceans) has an even wider and more discontinuous distribution, species living in South Africa, Australia, New Zealand, Malaya, Chili, Guiana and the West Indies. Evolution alone can explain alike the extent and discontinuity of the distribution of these animals. On the other hand a group of recent origin, the guinea-pigs, has a very restricted distribution in South America.

The most convincing evidence of all comes from a study of the inhabitants of islands. Those near to continents, such as the British Isles, possess a fauna and flora practically identical with those of the mainland. Conditions are very different on oceanic islands widely separated from the nearest continents with which they have at no period been connected. The fauna, except in so far as it has been influenced by man, must have originated from species which could fly, or be transported by wind, on floating timber or by some other natural agency. Amphibians, for instance, to which salt water is fatal, are never found while flying animals, birds, insects and bats, are particularly abundant, though frequently, owing to isolation, new species have evolved.

The population of the Hawaiian Islands is of particular interest in this connection. It has been described

as "the richest, maturest, and at the same time one of the most extreme cases of a flora and fauna built entirely out of trans-oceanic waifs" (A. Gulick). The islands are of volcanic origin, 2,000 miles from North America, over 3,000 miles from Japan and more than 1,000 miles from any other islands of biological significance. The islands support a rich and varied fauna and flora comprising very many species unique to the islands, the snails and the land birds being of especial interest. Of the former there are no less than 970 unique species or races, 417 of which belong to one distinctive family and 192 to another (which probably arose from the first). The first of these must have originated from a single species, probably of microscopic size for there are many land snails so minute that they can be carried for vast distances through the air, but at the present day it contains microscopic species and others three inches in length.

The most interesting group of birds, consisting of eighteen genera and forty species, must all have descended from some form of tropical American honey creeper. These have evolved in many directions, there are species adapted for feeding on insects, solid seeds, hard sandal nuts, fruits, boring insects and nectar. Indeed they have become so specialized that many are apparently doomed to destruction owing to the changes in the environment brought about by cultivation and the introduction of cattle and of the mongoose. In all, new groups of birds must have been introduced into the islands not less than nine times, including a rail which has since lost the power of flight.

Comparative anatomy, embryology, palæontology and geographical distribution, all were fitted in to that closely knit web of reasoning with which Darwin convinced the world of the fact of evolution. In all of these departments of biology more recent developments have done no more than confirm the soundness of Darwin's general deductions. But additional evidence has been forthcoming of recent years from new sources, the study of comparative physiology has revealed that the four blood groups into which men are divisible are also present in apes, that there is, indeed, an actual blood relationship between man and his nearest living animal relatives. And in many other ways the facts of comparative anatomy are being reinforced by those of comparative physiology. Even comparative parasitology plays its part in the accumulation of evidence. Since internal parasites are largely transmitted from one generation to another and as both host and parasite may suffer evolutionary change, it follows that close relationship between the parasites may indicate similar relationship between the hosts. This statement has to be qualified because parasites, particularly external ones, may pass from one animal to another of quite a different type.

But all this evidence, both what Darwin knew and what has been added since, would fail to carry conviction were it not for the fact of variation. The mechanism of inheritance ensures, as we have seen, that like shall beget like. But this stabilizing mechanism is offset by a perpetual tendency to change, equally characteristic of living matter, which is apparently

particularly powerful in certain animals and at certain periods in their history. This tendency for like to beget *unlike* is known as variation. It provides the mechanism whereby new forms of life have come into existence.

The fact of variation had, of course, been known ever since man, after first domesticating certain types of animals, had found it possible, by selecting suitable individuals for breeding, to fix in the offspring certain characteristics of value to him, thickness of the fleece in sheep, for instance, or yield of milk in cattle. Darwin laid particular stress on the results of such artificial breeding a good deal more than a modern writer would do, but he was able to demonstrate that variation does occur and that there is good reason for believing that it is an expression of that inward instability of living matter which has made evolution possible. Darwin then proceeded to indicate how suitable variations *might* be retained and finally incorporated in the make-up of all the members of the species. It was his second, though possibly less enduring, success that his explanation, unlike those of earlier writers on evolution, was widely accepted.

3 The Causes of Evolution

The presumptive evidence in favour of evolution is rendered irresistible by the fact of variation. It now becomes necessary to consider the nature and origin of this motive force in evolution, and the most convenient way of doing this is to consider first of all Darwin's

own views on the subject and then to review these in the light of modern knowledge.

Darwin divided variations into three types. The first he called 'single' variations or sports but they are better described as discontinuous variations, they are rare but produce striking differences between the individuals in which they occur and other members of the species. His second group consisted of 'individual', or better continuous, variations, which are of universal occurrence being represented by those slight differences which always exist between members of the same species. Finally he recognized a third group of 'definite' variations which he regarded as the result of environmental factors or of the habits of the individual.

Of these Darwin, decided that the second provided the great bulk of the raw material for evolution. The first type he dismissed, after much consideration, as being of such infrequent occurrence that they were certain to be swamped by interbreeding with normal members of the species. It must be remembered that he knew nothing of Mendel's work and so was ignorant of the law of segregation. The third type he accepted, to a lesser degree than the second and with some misgivings, as a factor in evolution.

He had now to determine the method whereby these innumerable slight variations, affecting every part of the organism, were able eventually to bring about the evolution of one form of life from another. He had been greatly impressed in reading Malthus' book on Population by the remarkable fecundity of animals. If all the millions of eggs produced annually

by a single oyster or a single sea urchin were to reach maturity the sea would soon become one solid mass of these creatures. Even in the very slowly breeding elephant, Darwin calculated, on the assumption that each pair produced six young during their lives, the descendants of a single pair would number fifteen million after five hundred years if they all reached maturity and bred. Yet despite this vast potential power of increase the numbers of different species do not normally fluctuate very greatly; they certainly do not increase unless transported to a new habitat. There must, Darwin considered, be a continuous struggle for existence, particularly intense between members of the same species, less intense between members of allied species and less intense again in more remotely allied species.

It was in this struggle that Darwin found the solution to his problem. It appeared to him that any variation which gave to its possessor an advantage over its competitors, no matter how slight, in the struggle for existence, would significantly increase the chances of survival of the individual. This would then be able to breed and so to hand on this favourable variation to its descendants which would, in time, replace the original type. In this way new species would be formed. Darwin called this process Natural Selection in contradistinction to the artificial selection of domestic animals so successfully practised by man and the results of which he advanced as a potent argument in favour of his views.

Natural Selection could not, of course, account for the appearance of variations; Darwin was well aware

of this (though this is one of the stock arguments against Darwinism) but he regarded it as a sieve through which all variations were strained, those which were advantageous alone being retained and so transmitted. For variations themselves he had no satisfactory explanation, he considered that they arose by chance and at random. The controlling factor was external to the organism and not within it.

This was the working hypothesis, as Huxley described it, which Darwin put forward to account for evolution. It met with immediate success because it was the first really credible explanation of the process the arguments in favour of which he had expounded with such skill. It is noteworthy that despite the very great advance in knowledge, particularly in heredity, since Darwin's time, it is still worthy of the most serious consideration.

The discovery and development of Mendel's work has fundamentally altered our ideas about variations. First place is now generally given to those 'single' or discontinuous variations which Darwin felt obliged to dismiss. We know now that these are the result of changes in the genes controlling the characters which they affect. Instead of being swamped by crossing with normal individuals of the species they are inherited in the usual Mendelian manner, appearing in the first filial generation if dominant to the original, unaffected genes, failing to appear if recessive and appearing partially if neither dominant nor recessive, but in all cases segregating out in the gametes. The mechanism of segregation is, in fact, the perfect means for preserving any such variation.

It is usual now to speak of such variations as mutations. This name was introduced by a Dutch Botanist, Hugo de Vries, who in 1886 found wild specimens of the evening primrose, *Oenothera lamarckiana*, which departed in various ways from the normal type. He bred numerous other generations and in all obtained some 800 different varieties which he described as mutations. Since that time many other cases have been investigated, notably by Professor T. H. Morgan and his school in their intensive study of *Drosophila*. More than four hundred of these have so far been observed and their inheritance studied, and it is indeed in this way that the chromosome maps already referred to have been constructed, for this is only possible when two modifications of the same gene are available for crossing. These mutations all affect external characters (or at least in part) such as eye colour, presence or absence of bristles, colour, or, more profound than these, presence or absence of wings (see Fig. 46). They do not appear very frequently, one in from five to ten thousand flies, excepting mutations which affect life and so prevent the young from developing. It is only the untiring work of Morgan and the rapid breeding of his admirably chosen

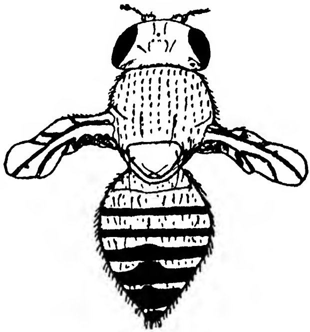


Fig. 46.

Drosophila with vestigial wings, a mutant (after Morgan).

experimental material which have enabled this knowledge to be gained.

It has also been discovered that the rate of mutation may be greatly increased in *Drosophila* and other animals and plants by exposing them to X-rays—by about 150 times in the case of *Drosophila.* Exposing the eggs of this animal to heat sufficient to kill most of them has given similar results with the surviving eggs. There seems no doubt that the genes are not stable, though they vary in this, certain mutations occurring more frequently than others, and it is the considered opinion of Morgan and of many of the other leading geneticists of the present day that mutations are *the* raw material of evolution.

This opinion receives important support from investigations into the nature of Darwin's 'individual' or continuous variations. These are now generally regarded as not inheritable but as no more than fluctuations in the appearance of a character which can normally be departed from for a certain distance in either direction. For instance the examination of large numbers of any one species will reveal differences in the length of the body or in any part of it, but the great majority of individuals will be of medium length, very few being extremely long or extremely short. Now so long as the stock is genetically pure for this character (that is if we are not dealing with allelomorphs for body length) then no matter whether we breed from medium, long or short-bodied animals we shall obtain the same range in size in the next generation. No amount of selecting of such

continuous variations will affect the size of the offspring.

Such, at any rate, is the confident belief of those who are convinced that mutations alone are responsible for evolution. But there are still certain biologists who consider that, if given time enough, evolutionary changes may be brought about by the selection of continuous variations. They cannot prove their case because their experiments would involve the vast periods of time which they postulate, but they base their case to a large extent on the undoubted fact that many mutations which have appeared in particular under experimental conditions are either of no particular value one way or the other to the animal—such as changes in eye colour—or else, like loss of wings in *Drosophila*, are definitely harmful. Such an animal would stand not the least chance of survival in nature. The upholders of mutations agree that many mutations do indicate a downward rather than an upward process but they counter their opponents' criticisms by arguing that the wild individuals are, as a result of long periods of selection, probably very highly adapted indeed and that almost any change (which would stand no chance of survival in Nature) must make its possessor less fitted for life in its environment. They are, in other words, almost as perfect as they can be. Moreover they point out, with perfect truth, that the characters of the wild individuals are inherited in the same way as the mutations which appear in captivity. Finally they argue that some of the mutant characters are at least as suitable as the

original characters of the wild individual and (so far as one can judge) would give their possessors just as good a chance of surviving under natural conditions.

There is, however, only one satisfactory way in which the upholders of mutations can establish the truth of their contentions. That is by the appearance, under experimental conditions and as a result of mutations, of a new species—of a group of individuals which though fertile amongst themselves will not breed with the species from which they sprang. Vigorous attempts are being made to satisfy this crucial test and though no success has as yet been made with animals, in plants a primula hybrid (*P. kewensis*) has been produced which does appear to satisfy requirements.[1] It is fertile and, in the great majority of cases, breeds true, but it cannot be crossed with either of the species from which it sprang (*P. floribunda* and *P. verticillata*). It is not at all improbable that the case for mutations will be finally established; we may even eventually see the production of new species at will by man. Certainly a supreme triumph should it come to pass.

There remains to be considered the third type of variations, Darwin's 'definite' type, the result of environment and habit. These Darwin took over from Lamarck, a French biologist (1744-1829) who believed in evolution and attempted to account for it by postulating that changes produced during the life of the individual are inherited. These changes are usually

[1] See *The Causes of Evolution*, by J. B. S. Haldane for a full description of the origin of *P. kewensis*.

called acquired characters or else modifications. They occur as a matter of common experience in ourselves. Thus a manual labourer will develop, as a result of his constant physical exertions, more powerful muscles than will a clerk, a man who goes bare-footed will acquire a thick layer of skin on the soles of his feet absent from the feet of men who habitually wear boots, white men who go to live in the tropics quickly become pigmented owing to the intensity of the sunlight.

A classic case of the effect of environmental conditions is provided by the results of an experiment carried out by the French Botanist, Bonnier. He divided a plant of the common dandelion into two equal parts and grew one on a mountain and the other in a valley. The former developed into a stunted plant with a long, massive root, the latter into a typical individual with long leaves and flower stems and with short, slender roots. During the course of the Great Barrier Reef Expedition certain corals (which grow in a manner very like that of plants and, like these, survive with ease division into various parts) were divided and the halves exposed to varying conditions. It was found that the halves of corals which normally lived in sheltered water and which were placed in more turbulent water never attained the same luxuriance of growth as their companion halves which were replaced in the normal, sheltered habitat.

Such modifications are acquired as a result of definite stimuli, provided by the habits of the organism, or by the environment, albeit the capacity to make the responses must be present in the organism. An

observation of the writer's on the shipworms which have already been described in some detail illustrates this point rather well. There is a giant species attaining a length of some five feet which occurs in the South Seas. This lives in mud (it probably begins life in wood in the usual way) encased in a limy tube which extends at the posterior and into two projections which enclose the siphons. In the other species a limy coating is laid down inside the burrow, except at the anterior end and that also becomes covered when the animal finally stops boring, but the siphons have no calcareous case. It was found, however, that if wood containing shipworms was placed in still water with the openings of the burrows pointing upwards, the fragments of wood which are continually being extruded formed a small mound over the opening and that when this was removed after several weeks the siphons were found encased, as in the giant shipworm, with limestone. What might, therefore, have been not unreasonably considered as a specific character in the larger species was actually merely a response to environmental conditions—the surrounding mud which threatened suffocation unless the siphonal openings were kept clear—and the common British species reacted in exactly the same manner when exposed to essentially similar conditions.

What acquired characters represent is actually the difference between the genotype and the phenotype—between potentialities and actualities. What Lamarck and his followers would have us believe is that they are inherited. Owing to their constant appearance in the

life of the individual in successive generations they so influence the mechanism of inheritance, it is argued, that eventually they appear in new generations which are not exposed to the original stimulus. Great stress is also laid on the effect of disuse, for instance the poor development or in some cases complete absence of eyes in animals which live in caves or burrows or in the abyssal regions of the sea where light is absent.

The inheritance of acquired characters appears on the face of it reasonable enough, indeed many people have apparently accepted it because it appeared to them 'common sense'. Were it true it would certainly provide an easy and readily intelligible explanation of evolution. But in point of fact there is, despite innumerable attempts to provide it, no satisfactory experimental evidence in support of the inheritance of acquired characters. Nevertheless it cannot be denied that, given time enough, the constant appearance of a certain character in innumerable successive generations *may* affect the genetical constitution of the race. More than this cannot be said, to say less would be unscientific; we know far too little about the origin of variations to say that acquired characters play no part in the process.[1]

This brings us to the consideration of the actual directive force in evolution. Are we to consider variations, as Darwin did, as occurring by chance and at random for no discernible reason, and then being

[1] The case for the inheritance of acquired characters is well stated by Professor E. W. MacBride in *An Introduction to the Study of Heredity*.

accepted or rejected by the external force of Natural Selection, or are we to consider that the appearance of variations is controlled by some internal cause which directs the future evolution of the race? In other words is Natural Selection fact or fancy?

There are certain biologists who, while accepting the external factor of selection, refuse to accept the Natural Selection of Darwin because, like the majority of biologists, they cannot accept his contention that continuous variations and not mutations form the raw material of evolution. The only difference between their selection and Darwin's is that the former acts on mutations, the latter on continuous variations. This distinction appears unnecessary. To Darwin, with his great contemporary, A. R. Wallace, belongs the credit of first indicating the probable importance of selection, a distinction in no way lessened by his failure, owing to the lack of certain knowledge now available, to decide upon the type of variation on which it acts.

But there are more weighty arguments against Natural Selection, as Darwin conceived it, than this. The study of palæontology reveals that many groups of animals now extinct were apparently heading irrevocably for destruction for vast periods of time before this actually took place. The vast reptiles of the Cretaceous period developed more and more elaborate and fantastic armour until eventually they seem almost literally to have sunk beneath its weight, amongst the mammals many early types seem to have become extinct for similar reasons, *Gryphæa*, a bivalve

allied to the modern oyster, apparently became extinct because its shell coiled more and more until the animal must have had the greatest difficulty in opening it at all. The history of the ammonites, a group related to the modern octopods and cuttlefish though with an external shell, is a remarkable record of successive changes which could only lead finally to extinction. In the same way the past history of existing species, such as that of the horse, reveals a steady progression in the one direction, not this time to final destruction but to more and more complete specialization to which man himself has added the coping stone by the artificial selection of the race horse.

It does appear, therefore, that evolution may take place in a definite direction, that is that variations may appear not at random but in one direction only. Under these conditions Natural Selection cannot act, it cannot select when there is no choice for it to select from, it can only, should the direction of evolution be harmful, eventually destroy the race. Evolution of this type is known as Orthogenesis, or development in straight lines. Orthogenesis is a statement of fact rather than an explanation for we have no knowledge of the mechanism which underlies this type of evolution.

Other biologists refuse to accept Natural Selection because they believe that new species arise direct from old ones without any of the intermediate stages which belief in Natural Selection involves. Natural Selection may, of course, speedily wipe out the newly formed species if this is unable to compete successfully with allied species, but it plays no part, as Darwin thought

that it must do, in the actual moulding of the new species. There also remains the possibility, by no means to be neglected, that a mutation might appear which would prevent its possessor, possibly for mechanical reasons, from interbreeding with its fellows. If the individual in which it appeared was capable of self-fertilization, as are many plants though comparatively few animals, a new species might arise in this way. Such an occurrence would clearly be much less frequent in unisexual organisms where the mutation would have to appear simultaneously in individuals of both sexes.

Natural Selection has also suffered at the hands of the more extreme of Darwin's followers who deliberately set out to discover a definite selective value in every character of a successful species. They frequently appeared oblivious to the probability, nay the certainty, that many of these characters have no particular value, in terms of the survival of their possessor, one way or the other.

When we turn to the evidence in favour of Natural Selection we find that it is much stronger than might have been expected, bearing in mind the date when the theory was elaborated and the great increase in biological knowledge which has since occurred. There is no doubt that selection does take place. There are two colour varieties of the praying mantis (an insect allied to the locusts and grasshoppers) one green and the other brown. Normally these live on similarly coloured backgrounds and it has been found that if green ones are tethered by silk threads to dead, brown grass and brown ones to green grass, these will rapidly

be destroyed by birds and ants, while individuals, similarly tethered, which blend in colour with the background, will be unaffected. The collection and subsequent care of 136 specimens of the common sparrow driven in an exhausted condition to earth after a violent storm revealed that the seventy-two individuals which survived were on the average not only larger than the others but also had wings nearer to the average, and therefore presumably most suitable, size for the species. These are but two out of many instances of selection in Nature. Whether it can accomplish all that Darwin claimed for it is much more difficult to determine. Of recent years, however, support for Natural Selection has come from a new and somewhat unexpected source. Evolution has been studied statistically and a mathematical theory of Natural Selection has been elaborated from the data so obtained which is strongly supported by those qualified to pass judgment upon it.

The general impression gained from this brief resumé of the evidence is that variations constitute the raw material of evolution, and that the case for discontinuous variations or mutations is much stronger than that for either continuous variations or acquired characters. Selection undoubtedly operates in Nature and it may be that Natural Selection operating on mutations rather than continuous variations, is the principal agency controlling the direction evolution takes. On the other hand there is far too much evidence of the presence of some inner directive force—some centre, shall we say, of germinal instability—

which controls the appearance of variations, as postulated by Orthogenesis, for this to be ruled out of court. It appears not improbable that evolution is controlled by some such inner force acting in conjunction with the external force of selection ; the case for Natural Selection is better than that for random variations.

However this may be, one important point is clear. Mutations which are to bring about significant evolutionary changes must have a very far-reaching effect on the organism. To return to the shipworms, it cannot be maintained, in the opinion of the writer, that the numerous adaptations which have fitted these creatures for life in wood have arisen separately and entirely independent of each other—the strain on the laws of chance is too great altogether. Moreover, the appearance of some of these adaptations without the others would unfit the animals for life in the original habitat without making life in the new environment possible. Evolution, as J. B. S. Haldane states, " must have involved the simultaneous change in many genes, which doubtless accounts for its slowness ". Certain special adaptations may well have arisen quite independently of any other character but it is quite otherwise with adaptations which involve changes in a variety of organs, as, for instance, in the shell, foot and adductor muscles of the shipworms, all of which are concerned in the mechanism of boring. We are driven to the conclusion that changes affecting any one of these functionally interdependent organs must have affected the others. This is possible of

explanation in either of two ways. The various characters concerned may be controlled by a variety of genes as interdependent as are the characters, or the genes may act independently of one another but a mutation which appears in any one of them will affect the characters controlled by the other genes not by way of the genes but by way of the character itself. There is nothing improbable about this because we know that different organs and tissues do influence each other during development, the fate of embryonic cells being frequently a result of their position in the embryo and not of their origin. The organism is a functional unit and mutations affecting more than very isolated characters (and even this may be an over statement) must influence the organism as a whole. We may even regard genes as chemical units and mutations as possibly due to slight rearrangements in their complicated molecules, but we must always think of evolution in terms of the whole organism and not of its constituent parts.

4 The Course of Evolution

Our knowledge of the results of evolution is based on the study of organisms living at the present time and of the fossil remains of extinct species. From this the course of evolution can, in broad outline, be deduced. The multiplicity of form characteristic of living things drove man very early in the history of biology to devise schemes of classification. The earliest of these were based largely on external resemblances but even in the

fourth century B.C. it was shown by Aristotle that animals must be classified on more fundamental characters. His examination of the comparative anatomy of the vertebrates revealed, as we have already seen, that whales and porpoises, for all their resemblance to fish in external form and habit, are actually mammals specialized for life in the sea. He drew up a broad classification of the animal kingdom dividing this first into sanguineous and exsanguineous animals, which corresponded to our modern distinction between vertebrates and invertebrates. He subdivided these into smaller groups, with considerable accuracy in the former but not very successfully in the latter. It was a long time before it was realized that the vertebrates are equivalent not to the invertebrates as a whole but to each of the great groups which constitute these.

Knowledge about the diversity and structure of animals increased greatly after the rebirth of enquiry in Europe at the time of the Renaissance, the invention of the microscope at the beginning of the seventeenth century and its exploitation at the hands of the classical microscopists, the Italian, Malphighi (1628-94), the Dutchmen, Leeuwenhoek (1632-1723) and Swammerdam (1637-80) and the Englishman, Hooke (1635-1703), revealing the presence of an hitherto unsuspected host of microscopic animals and the elaborate internal structure of insects and other minute animals. But classification lagged behind. The Swede, Karl Linnaeus (1707-78), a born classifier, made notable advances by his establishment of descending grades—classes,

orders, genera and species—and most of all by his introduction of binomial nomenclature. Every species since his time has been given a double name, the first being that of the genus, the second that of the species. Thus the lion is *Felis leo* while the tiger and the domestic cat, both members of the same genus but distinct species, are known respectively as *Felis tigris* and *Felis domesticus*. Linnaeus' description of animals and plants was contained in his *Systema Naturae*, first published in 1735 of which the tenth edition (1758) has been accepted as the basis of modern nomenclature. In his broad classification of the animal kingdom, Linnaeus went no further than Aristotle, dividing it into only six classes, mammals, birds, reptiles, fishes, insects and vermes (worms), all of which he considered of equal standing.

It was left to the supreme comparative anatomist, Cuvier (1769-1832), and to the first of the modern evolutionists, Lamarck (1744-1829), to make the great advances which constitute the essential difference between modern classification and that of Linnaeus. The former divided the animal kingdom into four 'embranchements' vertebrata, mollusca, articulata, and radiata, each consisting of animals constructed on a common ground plan. It was the conception of a comparative anatomist and, particularly in the case of the mollusca and articulata (jointed and segmented animals), represented a great advance. Lamarck conceived of the animal kingdom as a ladder stretching from the simplest forms to the mammals and culminating in man. He accordingly divided it into no

less than sixteen classes beginning with the infusoria, as he called the protozoa, and concluding with the mammals. He separated his four vertebrate classes, fish, reptiles, birds and mammals, from the twelve invertebrate classes.

Further work on comparative anatomy led to significant improvements in classification during the nineteenth century but the most important advances were due to research in embryology. As a result barnacles were transfered from the mollusca to the crustacea, and the frogs, newts and their allies separated from the reptiles and established as a separate class, the amphibia. The work of the Englishmen, Ray Lankester and Bateson, and of the Russian, Kowalewsky, on the development and structure of the sea-squirts (see Fig. 48) and other lowly relatives of the vertebrates, led to the establishment of the chordata to include these and the true vertebrates. The collection and description of ever-increasing numbers of animals led to an increase in the number of grades in classification, that of family (between the Linnean order and genus) being introduced by Batsch in 1780, that of phylum, which took precedence of class, by Haeckel in 1866 and that of grade itself as the primary division of the animal kingdom by Ray Lankester in 1877.

The classification of the animal kingdom into grades, phyla and the more important classes, as generally accepted at the present day, is given below, small groups of somewhat doubtful standing alone being omitted.

ANIMALIA

Grade A.

Phylum I.	PROTOZOA.	Non-cellular animals which may form aggregates but never tissues.
Class 1.	Rhizopoda.	Protozoa which move by means of 'pseudopodia' which display amoeboid movement, e.g. *Amoeba*.
Class 2.	Flagellata.	Protozoa which move by means of flagella.
Class 3.	Infusoria.	Protozoa which move, or feed, by means of cilia.
Class 4.	Sporozoa.	Protozoa with no special means of locomotion, reproduce by spores and are parasitic, e.g. the malarial parasite, *Plasmodium*.

Grade B.

METAZOA. Multicellular animals which possess tissues

Phylum II.	PORIFERA.	The sponges, distinguished from the remainder of the Metazoa, known collectively as the Enterozoa, by the presence of internal flagellated chambers instead of a true gut or enteron.
Phylum III.	COELENTERATA.	Distinguished from the succeeding phyla by the presence of two cell layers instead of three.
Class 1.	Hydromedusae.	Including the hydroid polyps, the siphonophores and probably the extinct graptolites.
Class 2.	Scyphomedusae.	The large jellyfish, etc.
Class 3.	Anthozoa.	The sea-anemones, stony corals, horny corals, etc.
Phylum IV.	CTENOPHORA.	Freely-swimming marine animals resembling jellyfish.
Phylum V.	PLATYHELMINTHES.	The flatworms, unsegmented with relatively simple structure.
Class 1.	Turbellaria.	Free-living flatworms.
Class 2.	Trematoda.	The parasitic flukes.
Class 3.	Cestoda.	The parasitic tapeworms.
Phylum VI.	NEMATODA.	The round or thread worms, many parasitic.

Phylum VII. NEMERTINA.	More complex worms, largely marine.
Phylum VIII. CHAETOGNATHA.	The arrow worms, all marine.
Phylum IX. ROTIFERA.	The wheel animalcules, very minute but relatively highly organized.
Phylum X. ANNELIDA.	The segmented worms.
Class 1. Archiannellida.	Small, primitive types.
Class 2. Polychaeta.	The common marine worms.
Class 3. Oligochaeta.	The earthworms.
Class 4. Hirudinae.	The leeches.
Class 5. Myzostomidae.	Leaf-like external parasites.
Class 6. Gephyrea.	Marine annelids without segmentation in the adult condition.
Phylum XI. ARTHROPODA.	The jointed-limbed animals.
Class 1. Onychophora.	Including species of the archaic genus *Peripatus*.
Class 2. Chilopoda.	The centipedes.
Class 3. Diplopoda.	The millipedes.
Class 4. Insecta.	The insects, characterized by three pairs of legs and often known as Hexapoda in consequence.
Class 5. Arachnida.	The spiders, scorpions, mites and ticks.
Class 6. Trilobita.	An extinct group.
Class 7. Crustacea.	The lobsters, crabs, prawns, woodlice, etc.
Class 8. Tardigrada.	The microscopic water bears.
Class 9. Linguatulida.	A small parasitic group.
Phylum XII. MOLLUSCA.	Unsegmented animals with frequently a ventral muscular foot and a fleshy mantle which often secretes a calcareous shell.
Class 1. Amphineura.	Including the chitons.
Class 2. Gastropoda.	The univalves or snails.
Class 3. Scaphopoda.	The tusk shells.
Class 4. Pelecypoda.	The bivalves.
Class 5. Cephalopoda.	Octopods, cuttlefish and squids.
Phylum XIII. POLYZOA.	The sea-mats, very small animals, usually colonial and all aquatic.
Phylum XIV. BRACHIOPODA.	The lamp shells, superficially like the bivalves molluscs with which they were long classified.

Phylum XV.	ECHINODERMATA.	Radially symmetrical animals with very characteristic structure, exclusively marine.
Class 1.	Cystida.	An extinct group.
Class 2.	Blastoidea.	An extinct group.
Class 3.	Edrioasteroidea.	An extinct group.
Class 4.	Crinoidea.	The sea lilies or feather stars.
Class 5.	Asteroidea.	The starfishes.
Class 6.	Ophiuroidea.	The brittle-stars.
Class 7.	Echinoidea.	The sea-urchins, heart-urchins and cake-urchins.
Class 8.	Holothuroidea.	The sea-cucumbers and beche-de-mer.
Phylum XVI.	CHORDATA.	Bilaterally symmetrical animals with central skeletal axis or notochord at some stage in development, with dorsal central nervous system in form of hollow tube and with gill-slits in adult or embryo.
Sub-Phylum	HEMICHORDATA.	Including the worm-like *Balanoglossus*.
Sub-Phylum	UROCHORDATA.	The sea squirts.
Sub-Phylum	CEPHALOCHORDATA.	Including the lancelet, *Amphioxus*.
Sub-Phylum	VERTEBRATA.	
Class 1.	Cyclostomata.	The lampreys and hagfish.
Class 2.	Pisces.	The cartilaginous fish (dogfish, sharks and rays) and the bony fish (cod, herring, etc.).
Class 3.	Amphibia.	Frogs, newts, etc.
Class 4.	Reptilia.	Snakes, lizards, crocodiles, tortoises and turtles.
Class 5.	Aves.	Birds.
Class 6.	Mammalia.	Kangaroos, sloths, dugongs, whales, horses, lions, rats, moles, bats, monkeys, apes and man.

The groundwork of this great scheme of classification was laid, in great part, by men such as Aristotle, Linnaeus and Cuvier who had a very different conception of the animal kingdom from that which now prevails. They all believed in the fixity of species and

so regarded the organisms they classified as constituents of a static system and not of a dynamic one as we do to-day. They were able, therefore, to envisage the ultimate establishment of a clear cut classification which would prevail for all time. The modern biologist who finds in evolution the only conceivable explanation of the origin of animals and plants now living can hope for no more than a useful, indeed for practical purposes an essential, classification of organisms as they happen to exist at the present time (or, in the case of extinct species, as they existed at the particular time when they were preserved in fossil form). The whole scheme of classification is an elaborate fiction, an attempt by man to dam up and fix the continually moving waters of evolution.

There are only two criteria of value in classification, one at the top, the other at the bottom, of the series of grades. Phyla consist of groups of animals constructed on the same ground plan, as revealed by the work of comparative anatomists and embryologists, while species, as defined by Linnaeus, are groups of animals which interbreed with one another. The great phyla are now established with universal consent, though we are still uncertain about the exact position of certain small groups, to which of alternative phyla they should be allocated or whether they ought to constitute distinct phyla of their own. The Linnean criterion of species is excellent, but unfortunately it can only be applied to a minute fraction of the six hundred thousand and more species of animals which have up to the present been described. The great majority of these are

distinguished by superficial differences in structure which may or may not be indications of a true specific difference in the Linnean sense.

There are no criteria whatsoever for the grades of classification between phyla and species, and difficulties increase as the descent is made from class to order then to family and finally to genus. None of these is capable of definition and their establishment and extent depends on no more than the considered judgment of the systemmatist. But imperfect as it is, and in the nature of things must always be, the classification of its subject matter is essential to the progress of biology.

The presence of this classification, for all its imperfections, enables us to survey with ease the broad expanse of the animal kingdom. Moreover, as it has been well expressed, it is " in its mixture of irregularity and system, exactly what would be expected if the animal kingdom owed its nature to a chain of contingencies stretching back to the beginning of life on the earth " (D. M. S. Watson). The whole can be compared with nothing more aptly than with a tree the tips of the terminal branches of which are alone boldly displayed, the trunk and the branches with their numerous subdivisions being occasionally faintly outlined, more often invisible. We may now with the aid of such evidence as is available fill in, not without profit to ourselves, the outlines of some of these branches.

It is usual to regard the protozoa as corresponding, more closely than any other modern forms, to the

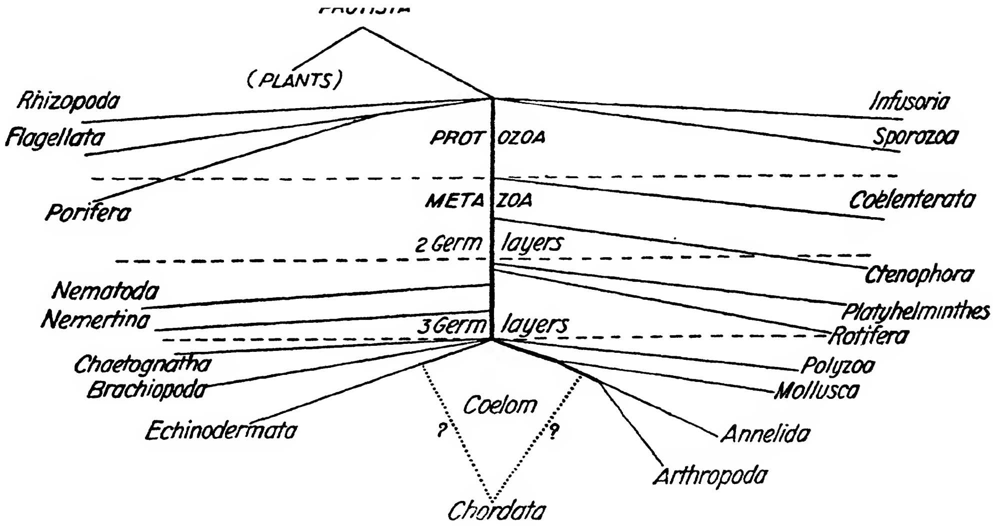


Fig. 47.

Diagram indicating the possible relationships between the various groups of the animal kingdom. The various modern phyla (and classes in the case of the protozoa) have been arranged in a semi-circle to indicate that they are all equally removed in time from their common ancestors. The horizontal broken lines indicate the divisions between the principal stages in evolution of complexity, the metazoa being divided into those with only two germ-layers, those with three but without a true coelom, and those with a coelom.

most primitive animals. It is by no means improbable that these primitive animals were unicellular but it is far less likely that they resembled even the least specialized of modern protozoa, such as *Amoeba*, which are as remotely divided from them in time as is man himself (this will best be realized by reference to Fig. 47). It is certain that the protozoa have evolved along lines essentially different from the metazoa, specializing within the cell-membrane, instead of forming tissues composed of specialized cells. The present range of complexity within the protozoa is very great, in respect of feeding alone some draw food to them in currents set up by ciliary action, others are predacious carnivores, others herbivores, some of them capable of perforating the stems of plants by mechanical or chemical means, while the whole class sporozoa consists of very highly specialized parasites.

The metazoa arose from at least two sources. The sponges are characterized by the possession of a particular type of flagellated cell known as a collar cell. These are also characteristic of a certain group of the class flagellata of the protozoa and it is not unreasonable to assume that the sponges represent evolution from aggregates of these. All the other metazoa may well have had a common origin and this, as already stated, may have come about as a result of a similar aggregation but quite possibly as a result of a subdivision, by the appearance of cell membranes, of multinucleate but non-cellular organisms.

The coelenterates are more simple in structure than the remaining metazoa. They possess only two of the

three germ-layers, external ectoderm and internal endoderm, found in these other animals. It is therefore reasonable to assume that they represent an early offshoot from the main trunk of evolution. They are a large and successful group which make up for their surprisingly slight variability in structure by their capacity to form colonies the constituents of which are specialized for various functions, some for feeding, some for defence, others for reproduction. They have acquired the power to form skeletons of calcium carbonate or of horny material, the prevalence and immense size of coral reefs bearing testimony to their success.

The simplest modern animals which possess the three germ-layers, mesoderm between the ectoderm and the endoderm, are the flatworms or platyhelminthes. Many of these have taken to a parasitic existence (practically unknown amongst the coelenterates). The cestodes, or tapeworms, represent the final stage in this process and they emphasize by their lack of organization—they possess no organs of feeding, digestion, or circulation absorbing the already digested food from the gut of the animal in which they live, the only well-developed system being that of reproduction—one very important aspect of evolution. This involves change but it does *not* necessarily involve increase in complexity. The latter certainly occurs when an animal becomes adapted for an active, free-living existence under new, and possibly more stringent, conditions, but the reverse happens when it becomes adapted for life under easier conditions, when it throws

the burden of food collection and food digestion upon some other animal as does the tapeworm.

The annelida represent a very great advance in evolution. They are 'coelomate' with a well-developed body cavity, have a head which bears the mouth, the major sense organs and, associated with these, an accumulation of nervous tissue from which the central nerve cord extends down the length of the body. A part of the coelomic fluid is specialized as blood which flows through a circulatory system, and in association with this numerous nephridia are present. For the first time the body is divided into segments, serial repetitions of essentially similar parts, as it is in the arthropoda and, though less apparent in the adult, in the vertebrata. The arthropods certainly sprang from the same common stock as the annelida with which they were combined in Cuvier's classification under the articulata.

The arthropoda rank with the vertebrates and possibly the mollusca as the most successful of the phyla, while, by virtue of the immense size of the class insecta, they are by far the largest. Arthropods have evolved to the full extent that the presence of an external jointed skeleton and segmented appendages, similarly encased, renders possible. These appendages have been adapted for swimming and walking, as organs of attack and defence, for the capture and mastication of food. In the insecta wings are usually present but these are outgrowths from the sides of the thoracic region of the body and are not modified appendages. The development of trachea which carry air with its

contained oxygen direct to the tissues has undoubtedly rendered possible the great powers of flight possessed by insects, with the high metabolic rate that implies. At the same time it has, as we have already had reason to point out, limited their size. The insecta are the one group which still continues to battle with man for the mastery of the earth, and the small size to which they are condemned is a factor in their gradual defeat. Another is the limitations imposed by the external skeleton. The hands of man are indifferent tools in themselves but they are capable, at the direction of his brain, of constructing and using tools of every description. The insect and the crustacean possess in their appendages tools which can carry out one operation supremely well, they can do little else. Certain insects have made an interesting attempt to overcome the bondage of the external skeleton by evolving into communities, in which there is division of labour amongst the individuals. Thus in the termites, or so-called white ants, which construct great 'anthills' sometimes over twenty feet high, there are five different 'castes' or types of individuals. There are the king and queen, the latter sometimes of relatively immense size, which are specialized for reproduction and are the parents of the entire community. The queen may produce eggs at the rate of up to one thousand a day for long periods, running into years. Should death overtake the king or queen their place is taken by members of the community which are potentially capable of reproduction. The great bulk of the community is made up of sterile

individuals which are divided into workers which collect food, care for the king and queen and do all the general work, and 'soldiers' with enlarged heads and huge jaws. They presumably protect the community though their exact function is not always clear. But the evolution of social life amongst the insects, successful though it has been up to a point and fascinating though its details may be, has been from the standpoint of evolution a failure, it has led to a too intensive specialization with an accompanying degeneration in the nervous system.

The mollusca have exploited the possibilities of quite a different type of structure. They are unsegmented and have nothing in common with the arthropoda and only the earliest larval stage with the annelida. We may regard them as having sprung at some far remote time from the same genéral stock as the segmented worms. Although possessed of an external skeleton in the form of a bivalve or univalve shell they have not become dominated by this as have the arthropoda for it has been abandoned with success in several instances while the single ventral 'foot', a large fleshy organ, incapable of the precise work done by the specialized arthropod appendages, has been modified with complete success to serve a surprisingly large number of purposes. By its aid the common snails creep over the surface of the earth, the cockles progress by a series of hops over sandy shores, the razor shell burrows with astonishing rapidity into sand, the shipworms are able to grip the wood at the end of their burrows and so are enabled to bore, in the

pteropods, or sea-butterflies the foot takes the form of two wings with which these animals swim in the surface waters of the sea while in the octopods, cuttlefish and squids it constitutes the siphon through which water is forced violently when the animals swim. The range in complexity of structure within the phylum is very great including as it does sluggish limpets, sessile oysters and the very highly organized cephalopods.

There is an entire class, the pelecypoda or bivalves, which is specialized for feeding on minute particles carried in suspension in the water (see Fig. 2, p. 26). They are an extremely successful group with very standardized structure (the shipworms and one other group form the solitary exceptions) and are confined, as a result, to this particular mode of life. The brachiopoda or lamp shells which superficially so resemble them that for long they were classified with them are adapted for a precisely similar mode of life, a fact which explains their superficial resemblance to the bivalves. But they are a small group with many more fossil than modern species the result of their failure to evolve such perfect mechanisms for feeding and for the subsequent disposal of the food as the bivalves. The resemblance between these two groups, due to their mode of life and not to their origin, constitutes an example of *convergence* as does the superficial resemblance between whales and fish. Instances such as this reveal the impossibility of attempting to classify animals on anything but fundamental structure which is not affected by the mode of life.

The echinodermata have evolved on lines peculiar to themselves. The adults are, with few exceptions, radially symmetrical like the common starfish and sea-urchins. They have a unique means of locomotion by means of 'tube-feet', numerous tiny tubes with terminal suckers which are extended or drawn in by pumping fluid from a special 'water vascular system' in and out of them. That they have evolved from bilaterally symmetrical ancestors is revealed by the bilateral structure of their larvae. The resemblance of these to the larva of a primitive chordata (*Balanoglossus*) has led to the theory that the echinodermata and the chordata have a common origin, a view which has recently received some support from chemical analyses of their muscles.

The origin of the chordates is wrapt in obscurity. The alternative to the echinoderm theory is that they sprang from an annelid stock, a view which accounts for their segmentation but necessitates a radical re-orientation of the organs, notably a change from ventral to dorsal of the nerve cord. Amongst the primitive chordates the sea squirts are of especial interest. These possess a 'tadpole' larva (see Fig. 48) with a notochord, a dorsal, tubular nerve cord, a brain, eyes and gill slits—all characteristic of the chordates in general. But this active larva undergoes a retrogressive metamorphosis, turning into a sessile adult which consists of no more than a stout bag with two openings and containing a second bag of tissue through which water is sieved (by a mechanism analagous to those of the bivalve molluscs and the brachiopods, with

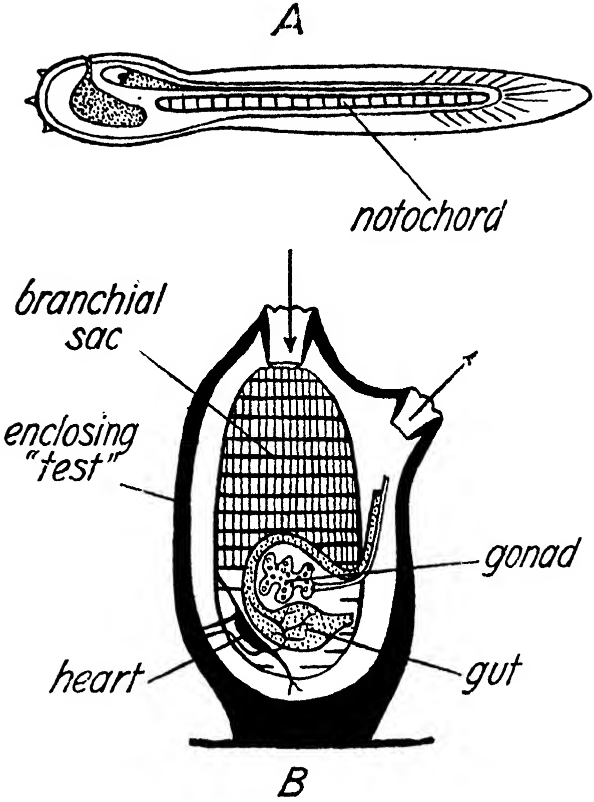


Fig. 48.

Semidiagrammatic representation of a larva or tadpole (*A*) and an adult (*B*) ascidian or sea squirt. The latter is attached and feeds by means of ciliary currents, the ingoing and outgoing currents being represented by arrows. The tadpole is very greatly enlarged. (*B* after Herdman.)

which these animals were formerly classified), a digestive and a reproductive system and very little else. The notochord, the nerve cord and brain (except for slight remnants) and the eyes of the larva all disappear. Without a knowledge of the development no comparative anatomist could possibly have classified the sea squirts in the same phylum as the vertebrates.

Although we know so little of the origin of the vertebrates we know, owing to the fullness of the geological record (see Fig. 45, p. 172), more about the evolution of their constituent classes, fish, amphibia, reptiles, birds and mammals, than about that of any other groups of animals. We know that each successive group sprang from unspecialized members of the preceding class, from the base and not the apex of the stock, and that after its successful establishment each class suddenly evolved in all directions, by a process of adaptive radiation, when the weight of competition from the preceding group, or of unfavourable environmental conditions, was released. But the study of comparative anatomy and of embryology tells us still more about the evolution of the vertebrates, it reveals that this was essentially the story of the conquest of the physical environment.

The first step was the emancipation from water to which fish were and still, with a few rare exceptions, are confined. This involved the development of limbs, organs of movement over land, of lungs, organs capable of extracting oxygen out of the air, and of a body covering which would prevent excessive loss of water. The amphibia made the first steps in this direction

but they were not entirely successful. The early stages of life had still to be spent in water and only at a certain stage did the larva exchange gills for lungs and develop limbs and become capable of living on the surface of the land. Moreover their soft, permeable skin was far from an ideal outer covering for a land animal The reptiles were the first group entirely to emancipate themselves from water. They laid eggs with a stout protective covering in which the embryos developed within a bag containing fluid known as the amnion and which was formed in the early stages of development by the embryo. Respiration and excretion were carried out through another structure called the allantois which led from the embryo to the inside of the permeable egg case. A plentiful supply of yolk enabled the embryo to develop the essential structures of adult life while still in the egg and to hatch out as a small, and very active, edition of its parents. The limbs were better constructed and enabled the reptiles to raise their bodies farther from the ground and so to move with greater rapidity and sureness than the amphibians. Finally the surface of the body was covered with strong, impermeable scales.

To the attainments of the reptiles the birds and mammals added the conquest of the effects of temperature. Their metabolic activities were carried out at the same optimal temperature no matter whether they lived in the Arctic regions or at the Equator. To insulate their bodies and so retain the heat generated within them they developed the one a covering of

feathers (clearly derived from the scales of reptiles) and the other of hair. With the aid of the feathers birds acquired a power of flight and a mastery of the air surpassing that of the insects or of the pterodactyls they superseded. This also involved the transference to the hind limbs of the function of walking hitherto shared by both pairs of limbs which involved radicle alterations in the hip girdle and the attachment of this to the axial skeleton. The development of the great pectoral muscles concerned with the movement of the fore limbs in the action of flight necessitated an improvement in the circulatory system which, in the birds, as in the mammals, is completely divided into pulmonary and systemic systems. The requisite amount of oxygen was obtained by the addition to the lungs of air-sacs.

In one particular the birds made no essential advance over the reptiles, namely reproduction. The eggs of a bird are essentially the same as those of reptiles but are larger and fewer in number because the birds care for their young which stand a correspondingly greater chance of survival than do the neglected young of the reptiles. It is in reproduction that the mammals have transcended the birds to which they are, in terms of intensity of metabolism and perfection of the sense organs in many respects inferior. The simplest mammals surviving at present are the monotremes of Australia, the duck-billed platypus, *Ornithorhynchus*, and the spiny anteater, *Echidna*. These two creatures lay eggs like birds and reptiles but they possess that essential characteristic of the mammals, mammary

glands, the milky secretion of which nourishes the young after they are hatched. In the marsupials the earliest stages of development are passed within the uterus of the mother but the young is born at a very early, and extremely helpless, stage when it is transferred to the pouch and remains there, obtaining nourishment from the teats of the mother until able to move about independently. In the remaining mammals, alone to be found over the greater part of the earth, viviparity is taken to the last degree, the embryo is nourished while in the uterus by way of a complicated organ called the placenta formed by the embryo and which grows into the tissues of the uterine wall. The young are retained within the body of the mother for a relatively much longer period than in the marsupials and are frequently born, as for instance in the goat, capable of immediate activity. In other cases, as in the cat or in man himself, they remain in a helpless condition for some time during which they are nourished by the milk of the mother and guarded with vigilance by both parents.

But in the last resort it has been the evolution of brain which has contributed most to the triumph of the mammals and enabled man, in which this line of evolution finds its highest expression, to conquer in his own person land, sea and air, heat and cold and almost every factor of the environment, to subject and exploit the animal and plant kingdoms. The descent of man can be traced with some degree of certainty from comparatively unspecialized arboreal mammals, possibly not unlike some of the modern insectivores,

such as the shrews, by way of the primitive primates (the final order of the class mammalia which includes the lemurs, marmosets, new world monkeys, old world monkeys, anthropoid apes and man). These ancestors of man lived in trees where they developed a more or less upright carriage, as a result of their habits which entailed the specialization of the forelimbs for reaching upward and grasping and of the hind for bearing the weight of the body. At the same time they acquired an opposable thumb without which the hand could not grasp (a similar development of opposible digits occurs in the tree-climbing chameleons amongst the reptiles). The sense of smell, so all-important to ground mammals, became of secondary importance and the sense of vision took its place. To this we may attribute the reduction of the snout region and also the development of binocular and stereoscopic vision so important in judging distances and enabling these animals to jump with certainty from branch to branch. We can certainly attribute to it important changes in the brain, notably in that part of the cerebrum known as the neopallium. The portions associated with vision and also with hearing, touch and the control of motor activities, all become increasingly developed in the series from the tree shrews through the lower primates to man, while the area of the brain concerned with smell, of supreme importance in the lower vertebrates and in the ground mammals, becomes correspondingly reduced.

Yet another result of arboreal life may have been the reduction in the number of young produced at any

one birth necessitated by the difficulty of caring for large numbers under such conditions. Certain it is that the conditions in man where it is the exception for more than one child to be produced at a time and where the young reach maturity very slowly has been a factor of the greatest importance in his evolution. The greatest possibilities for the further evolution of man lie in the possibilities of a further increase in the duration of pre-adult life.

The ancestors of man descended from the trees with all of his essential characteristics well developed. They were probably not at all unlike the modern apes which, though they certainly do not represent his ancestors, are probably descended from similar, if not identical, forebears. These early forms of man found themselves possessed of an exceptionally large brain and, in their forelimbs, no longer concerned with locomotion, and their hands, now capable of grasping, of perfect instruments for carrying out the diverse duties which growing intelligence suggested. The human hand, and though this has been mentioned before it is worthy of repetition, is supreme in virtue of its capacity to do so much; in its lack of specialization. The limbs of a horse are infinitely more specialized than the forelimbs of a man, but though they can do one thing supremely well, carry their owner with astonishing speed over a firm surface, they can do nothing else.

Gradually the discovery of fossil remains is filling in the story of man's more recent ancestry. We know of several now extinct genera which lie at or near the

stem which connects man with the ancestors common to him and to the apes, notably the ape man of Java, *Pithecanthropus*, and the Piltdown man, *Eoanthropus*. There are also a number of fossil skulls and other remains which are regarded as the remains of extinct species of the genus *Homo*, the Heidelberg man, *Homo heidelbergensis*, the Rhodesian man, *H. rhodesiensis* and Neanderthal man, *H. neanderthalensis*. All the existing races of man obey the Linnean test of a species, they can interbreed freely. The absence of pigment in the white races is regarded as of comparatively recent occurrence and it is probable that the Australian race is the oldest, the Negro next, then the Mongol and finally the white races which are subdivided into Alpine, Mediterranean and Nordic types, in the last of which reduction of pigment is carried to the furthest stage.

The final stages in the development of man, the acquisition of the power of speech, the development of communities, the increase in knowledge from generation to generation made possible first by oral tradition, then by the written word, and the consequent development of civilization, carry us beyond the scope of this book.

Chapter IV

THE ORGANISM IN NATURE

No organism lives unto itself. Nature is a unity, albeit complicated almost beyond description, and every animal and every plant plays some part in the economy of the whole. Just as each living organism represents a delicate balance of forces, so does nature ; just as the forces within the organism are perpetually changing, necessitating continuous readjustments to maintain the essential equipoise, so in nature from day to day, from season to season, from year to year and from era to era, organisms wax and wane and the balance of life is continually changing.

The study of living things in nature is known as ecology. This is really no more than a new name for what has long been known as natural history. It was Darwin's interest in natural history, for he was one of the supreme naturalists of all time, that made it possible for him to establish the truth of evolution. And yet, paradoxically, it was he who was thereby responsible for driving biologists from the study of nature to the laboratory there to spend laborious days and nights dissecting and sectioning dead animals or minute embryos interpreting their results in the new light which evolution had cast. It is only of recent years that the study of living things in nature has been

resumed. This, as we shall see, has been due in no small measure to economic necessity.

It has already been shown how animals are absolutely dependent on plants for the supply of organic matter from which alone they can obtain energy, while plants in their turn are dependent on the radiant energy of sunlight and on adequate supplies of carbon dioxide and water and of certain inorganic salts—notably those containing nitrogen and phosphorus—without which they cannot form proteins. Since there is seldom any serious lack of sunlight, except during the polar and temperate winter, and still more rarely of carbon dioxide, the limiting factor in plant life is usually the supply of nitrogen or phosphorus which is strictly limited. This explains the all-importance of these substances as fertilizers and why the nitrate deposits of Chili have been of such great economic value although these are now being displaced by nitrates formed synthetically from atmospheric nitrogen, a discovery which enabled Germany to maintain herself for four years when cut off from the rest of the world.

The cycle of events, inorganic salts→plants→animals→inorganic salts, is most clearly displayed in the sea, notably in the waters which surround our own coasts or those of any other temperate country. In midwinter there is a great paucity of life in the surface waters, there are abundant supplies of nutrient salts but both temperature and sunlight are at their minimum. In the early spring there is a sudden change, sunlight increases and there is a remarkable outburst of plant life. This consists of microscopic

organisms, principally diatoms and dinoflagellates, which drift about in the surface waters and constitute a part of what is known as the plankton (in contradistinction to the nekton, or freely swimming organisms of the mid-waters, and the benthos, which consists of the organisms which live on the bottom). The plants of the plankton form the true meadows of the sea, equivalent to the grass and herbage on land, for the sea weeds which line rocky coasts are too limited in quantity to play more than a very minor role in the economy of marine life.

After the spring increase in the plant plankton comes a similar increase in the animal plankton, minute animals with a similar distribution which feed upon the plant plankton. They consist very largely of minute crustaceans, though representatives of the great majority of the phyla are found in the plankton, either as minute adults or as freely-swimming larvae of fixed or bottom-living forms, such as barnacles and oysters or sea-urchins and worms. The plankton, directly or indirectly, forms the food of the great bulk of the animals in the sea. Bivalve molluscs, sea squirts, lamp shells and other fine-particle feeders live directly upon the plant plankton, fish such as herrings or mackerel and even the immense whale-bone whales feed on the animal plankton, while other fish, such as plaice or haddock, feed largely upon the bivalves, or, like the dogfish, on the herring. In one way or another the energy accumulated by the plant plankton in the sun-lit surface waters is passed on to the animals in the deeper waters and on the sea bottom.

The power of the sun increases steadily as the spring gives place to summer, but the plant plankton reaches its maximum in the late spring and then suddenly declines. The nutrient salts in the surface waters, where alone they are available to the plant

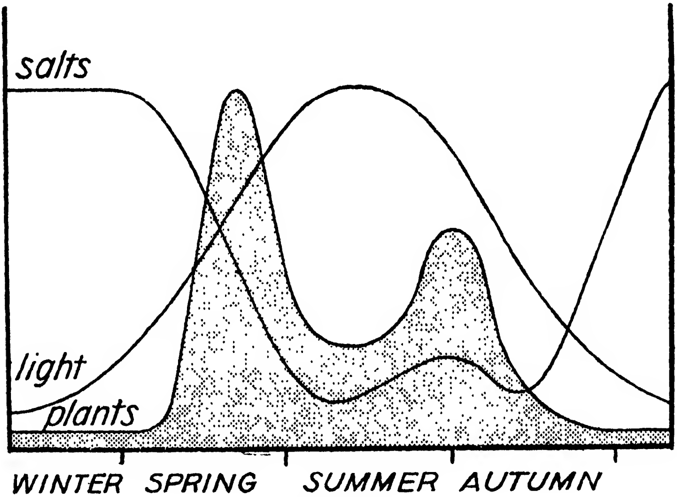


Fig. 49.

Graph indicating the changes in light intensity, concentration of nutrient salts (nitrates and phosphates) and plant plankton during the year in the surface waters around the coasts of Great Britain (modified after Russell and Yonge).

plankton which must have light, have become seriously depleted with inevitable consequences to the plants. There is still actually an abundance of these salts in the deeper waters but owing to its higher temperature the surface water floats on top of the colder

and so heavier deeper water and there is little possibility of mixing. In the autumn there is a second, smaller increase, in the plankton and then this declines steadily until it reaches its minimum in mid-winter.

But during the winter the stage is set for the next outburst of life in the spring. All the year the dead bodies of the plants and animals of the plankton and also of many of the animals which have fed upon them, have been falling to the bottom. There they decompose, the result of bacterial action, and, in a series of stages, the complex organic matter of which they are composed is broken down again to the carbon dioxide and water and to the simple salts—nitrates and phosphates above all—from which they were originally built up. In this way great new supplies of the all-important nutrient salts are formed. As the sun declines in power the surface waters lose their heat and a time comes when the water, at any rate in the comparatively shallow areas around our coasts, becomes much the same in temperature from top to bottom. The barrier to mixing is thus removed and the great storms of the winter ensure that the water is thoroughly stirred from top to bottom. In this way the surface waters receive a new supply of salts and when the spring comes a new outburst of planktonic life inevitably occurs.

In certain parts of the world a continual 'up-welling' of water from the depths of the ocean bearing with it abundant supplies of nutrient salts leads to an abnormal abundance of plankton and so of animals which feed on this. This occurs along the coasts of

southern California and is the explanation of the great sardine fishery for these fish are plankton feeders. An even more interesting state of affairs is found off the coasts of Chili and Peru, where deep currents from the Antarctic upwell. There is in consequence a great development of plant plankton, animal plankton is correspondingly abundant, great shoals of fish feed upon this plankton, and these in turn are preyed upon by immense numbers of sea birds which nest along the coast. In this way great deposits of guano have been and are still being formed and these are dug up and exported, some to this country, for use as fertilizers. So we in England may feed on plants which have been nourished by nutrient salts from the Antarctic which have come to us by way of currents through the depths of the Pacific, then through the bodies of plant plankton, animal plankton, fish, and finally birds, afterwards being transported across the Atlantic by steamer and possibly across half England by rail before being spread on English fields.

The interrelationship between plants and animals goes much farther than the fundamental dependence of animals on plants. As Darwin was careful to point out, the struggle for existence involves more than actual conflict, it also involves the assistance, unconscious but none the less significant, of one type of organism by another. Two instances, originally described by Darwin himself, will suffice to make this clear. The amount of clover in any region is dependent on the number of cats. The connecting links are provided by bees and mice. Clover is fertilized by bees, the

nests of bees are destroyed by field mice. It follows therefore that the more cats the fewer mice, the fewer mice the more bees, and the more bees the more clover. Again in his well-known book on earthworms Darwin was able to show how all-important are these lowly but ubiquitous animals. They burrow everywhere into the soil coming to the surface to eat leaves, the substance of which, after passing through the gut of the worms, is deposited in the burrows beneath the surface. In this way the soil is continually being enriched by vegetable matter which, on further decomposition, yields important nutrient salts. Good land contains some half a million earthworms per acre and they constitute an essential factor in its fertility. On land, therefore, if not in the sea, animals go far to repaying the plants which have made their existence possible. At the same time the assistance given by the worms to the plants is of assistance to the animal kingdom as well, for the number of animals in any region is dependent on the number of plants.

We must now take the plants for granted and consider the interdependence of animals. The ecologist, surveying nature as a whole, distinguishes various types of animal associations. Each of these is found in a particular environment and consists, it has been estimated, of usually not more than some 200 different species of macroscopic animals (in temperate regions). Thus in the sea characteristic associations are found, for instance, on sea shores between tide marks, on coral reefs in the tropics, in the abyssal depths of the oceans, while the plankton which drifts near the surface

constitutes another. Animals which live on the sea shore must be capable of withstanding very diverse conditions, exposure by the tides twice a day, the force of the sea, the effect of rain when the tide is out, extremes of temperature, and so forth. Despite the many qualifications needed for success in this environment it is one of the most densely populated, while shore associations are unique in the diversity of the animals which compose them. Moreover the populations of rocky shores are different from those of sandy shores which in turn differ from those found in the mud of estuaries.

Coral reefs are unique in that shore conditions are provided for a multitude of animals as a result of a characteristic property possessed by one of them, the remarkable skeleton-forming power of the corals themselves which can build up a massive reef of limestone, in some cases many miles from land, capable of withstanding the full force of the sea. Reef-building corals can only live where the temperature of the surface waters seldom falls much below 20 degrees C. and so are confined to the tropics.

The inhabitants of the great depths of the ocean live in the most remote of all environments, under immense pressure (they may be anything between two and six miles beneath the surface), in total darkness and at a temperature very near to freezing point. Plant life cannot exist in the absence of light and the abyssal seas are a backwater outside the main stream of life. The animals which live in these profound depths exist either on what drops down to them from the surface waters or else on each other. They

exhibit some of the strangest adaptations, immense jaws and stomachs which enable their possessors to swallow other animals larger than themselves, long, stalk-like legs for moving about on the soft mud bottom, a complete absence of eyes or else abnormally large eyes often situated on the end of long stalks, and frequently elaborate light-producing organs.[1]

The surface of the land provides an even greater range of environmental conditions with a corresponding increase in the number of associations. To mention only a few of the more obvious, there are deserts where the animal population (always present though naturally sparsely distributed) must be capable of withstanding lack of moisture and great extremes of temperature; tropical rain forests where life is overpoweringly prolific and there is unceasing competition, and where one association of animals is found in the depths of the forest, a population uncanny in its silence, and another on the tree tops in the bright tropical sunlight, a noisy fauna of chattering monkeys and screaming parrots. Even in our own countryside quite different associations of animals are found on heaths and marshes and even in oak woods and pine woods, while in each of these the animals to be found in the daytime give place at dusk to a very different fauna of nocturnal creatures, butterflies, sparrows and rabbits giving place to moths, owls, bats and hedgehogs.[2]

[1] For a general account of marine communities (including plankton) see *The Seas* by F. S. Russell and C. M. Yonge, and of coral reefs, *A Year on the Great Barrier Reef* by C. M. Yonge.

[2] See *Exploring the Animal World* by Charles Elton for a delightfully written account of animal ecology with especial reference to the British countryside.

These various associations are composed of most diverse assemblages of animals which literally occupy every niche and cranny. The more carefully they are studied the more strikingly is their interdependence revealed. This is obvious enough in the most extreme case of association, that of parasitism of one animal by another. Parasitism is widespread, there is hardly a group of the animal kingdom which does not include parasites, and probably hardly a single free-living metazoan which does not harbour parasites on or in its body, the vertebrates in particular have veritable communities of parasites within and upon them. Parasitism constituted a very real problem so long as animals were regarded as all of them created with a definite purpose or, as one still so often hears in general conversation, for some 'use', but it falls naturally into line with other manifestations of life when considered in terms of evolution. It is then seen to be a natural result of that process, and of the tendency of living matter to exploit every possible environment. The life-histories of parasites are frequently extraordinarily complicated. It is a matter of common knowledge that the malarial parasite passes part of its life-history in the red blood corpuscles of a human being and another within the body of a mosquito. Many tapeworms have an even more complicated existence, some passing a preliminary stage in the body of freshwater crustaceans, then, when these are eaten by fish passing into the body of the new host, and attaining the final adult condition in the gut of a carnivorous vertebrate, possibly a human being, which eats the fish.

It should be understood that parasitism, though at best a one-sided business the parasite alone obtaining any advantage, does *not* necessarily involve the death or even the ill-health of the host animal. This is not infrequently the case when a parasite attacks a new host, but in the course of time a balance is struck and, as we say, the host becomes tolerant to the parasite. Thus it is that the parasite of sleeping-sickness (a flagellate protozoan known as a trypanosome which invades first the blood stream and finally the cerebro-spinal fluid) is frequently fatal to man and domesticated animals but does no harm to the wild game which have been subject to it for a much greater period of time. It is actually much more destructive to natives of East Africa, where it has most recently appeared, than to those of West Africa where it has long been known. The establishment of tolerance by the host is just as much to the advantage of the parasite as to that of the host since the death of the host involves that of the parasite.

There is another type of intimate association between two different animals or between an animal and a plant known as symbiosis, in which the advantage is, at any rate to some extent, mutual. Among the most intimate associations of this type are between animals and unicellular plants. This is particularly common in the more simply organized metazoans, notably the coelenterates, which digest intracellularly, the plants having probably made their way into the tissues through the ingestive region of the gut. All reef-building corals contain literally millions of these minute

plants. The association is essential to the plants—they are never found free in the sea—and they obtain both protection and also abundant supplies of food because the animal, as a result of metabolism, is continually producing great quantities of carbon dioxide and also of salts containing phosphorus and nitrogen and these are available to the plant. The animals *can* exist without the plants, as individuals

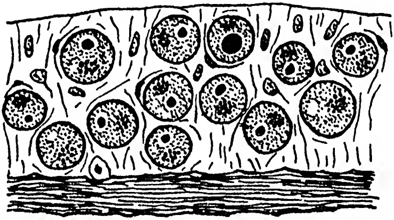


Fig. 50.

Portion of the endodermal tissues of a reef-building coral to show the great numbers of symbiotic unicellular plants invariably found in them (after Yonge).

at any rate. But there is, at any rate in the opinion of the writer, more than a probability that the amazing powers of growth possessed by corals and which have enabled them to build reefs and to maintain them despite the continuous battering of the sea, are due primarily to the automatic removal by the plants of the waste products of metabolism. In the absence of the plants these would only slowly escape from the tissues with a corresponding retardation of further metabolic activity.

There are many instances of symbiotic relationships between different animals. One very frequently quoted is that which exists between hermit crabs and anemones which fasten themselves on to the univalve shell in which the crab has taken up residence. The anemone is carried out by the crab and secures fragments of food which float away when the crab masticates its prey, the crab in its turn being protected in some measure by the sting cells with which the tentacles of the anemone are abundantly armed. An even more striking example of this type of co-operation between different kinds of animals is furnished by the giant anemones of Pacific reefs and little fish which are almost invariably to be found living within the shelter of their tentacles. The anemones may attain a diameter of almost two feet and are yellow, brown, green or blue in colour, the fish are one or two inches long with conspicuous orange bands running round the body. Such a habitat is almost the last in which one would naturally look for fish because the sting cells of the anemone are deadly weapons and any ordinary fish of the same size which came within reach of the tentacles would speedily be paralysed and then swallowed by the anemone to be digested within a very short space of time. But the anemone fish is immune to the poison and is actually protected, for it is a poor swimmer with no natural means of defence, by those very weapons which mean death to other fish.

The natural food of the fish consists of the animal plankton which drifts past the anemone but apparently when this fails the fish may, with perfect impunity,

bite pieces out of the tentacles of its protectors. But it gives something in return for the protection and food which its receives. It carries away or consumes food which has been rejected by the anemone and which would otherwise decompose and it may even on occasion bring food to the anemone, while, most remarkable of all, when the anemone is in bad condition, the fish may 'treat' it. It does this by rubbing against it and waving its fins in such a manner that a current of water is wafted over the drooping anemone.

The dependence of parasite on host and the interdependence of symbionts is obvious, but the interrelationships between the different members of all natural associations, though frequently much more difficult to determine, are fundamentally just as important. This is most clearly revealed by what happens when the balance of Nature is upset, usually by man, in any region. This may be brought about in one of two ways, by the destruction of any one animal or group of animals, or by the introduction of some particular animal or plant new to the environment.

The results of the destruction of animals are revealed, all too clearly, in Africa at the present time. Great plagues of locusts are doing enormous destruction to crops and foliage. In northern Africa the increase in locusts has been traced to the destruction of such birds as quails, partridges and small bustards, which live on these insects; a single quail, it is estimated, may eat about one thousand locusts daily. In the same way, in East Africa, the wholesale destruction of leopards by the natives, who obtain a good price for their

skins, has resulted in a great increase in baboons and wild pigs the numbers of which were formerly kept down by the leopards. So what the natives gain by the sale of leopard skins they lose by the destruction done to their crops by the swarms of baboons and pigs. And in time the leopards will be so reduced that little can be made out of them while the baboons and pigs will have multiplied still further with inevitable further destruction to crops.

Another striking example of the effect of the destruction of carnivorous animals on other members of the fauna comes from Norway. There is a bird called the willow grouse, not unlike the grouse of this country, which used to multiply normally every three or four years when it was shot for sport. After such good years the numbers decreased owing to the spread of diseases due to overcrowding. The Norwegians then destroyed large numbers of the mammals and birds of prey, such as foxes, martens, wolverenes, kites, eagles and sparrow-hawks. But it was found that the effect of this 'protection' from their enemies was to increase the mortality of the grouse due to disease. The suggested, and very probable, explanation is that under the old conditions grouse which were suffering from disease were speedily destroyed by their enemies because they were unable to fly properly and so could not escape. When this natural mechanism for the destruction of diseased individuals was removed, these were able to mix freely with the healthy grouse and infection spread rapidly, and with disastrous effects, throughout the entire population.

In any particular association, the members of which have been living together for long periods, a balance is struck, various natural checks preventing, except under somewhat exceptional cases, any untoward increase of any one species. But when man introduces a new animal or a new plant for which there may be no natural checks, this tends to run riot. The classic instance of this is provided by the importation of rabbits into Australia. These animals, which are naturally very rapid breeders, quickly spread like a plague over the temperate regions of that continent. They did immense damage to the grass which, as the food of sheep, is the most important natural product of Australia. Immense sums of money were spent in the vain attempt to destroy the rabbits. But it is interesting to note that the rabbit now has settled down in his new home and is actually becoming of some economic importance, great numbers of frozen carcases and bales of skins being exported annually. The rabbit is beginning to repay some small part of the money spent on his destruction.

New Zealand has suffered in a similar way. In this case particularly by the introduction from this country of starlings and blackberries. The starling, introduced originally owing to its associations with England, quickly became a plague and carried the seeds of imported blackberries far and wide. These established themselves and formed in many places great thickets which rendered agriculture impossible and even caused the destruction of lambs which become entangled in the thorns.

Widespread damage has been done in North America by the introduction of the gipsy moth from Europe. The caterpillars of this insect spread over trees, eating every leaf upon them and speedily reducing them to bare branches. A study of the moth revealed that its much greater abundance in its new habitat was due to the absence of the parasites which control its numbers in Europe, and which had not, as it happened, been present in the insects imported into America. These were introduced and the numbers of moths quickly declined. This method of controlling animal or plant numbers has become known as biological control, and it has been used with success in many instances. Great areas of Australia which for years past have been rendered useless by infestation with prickly pear (another importation) are now being cleared for agriculture owing to the action of an insect, appropriately called *Cactoblastus*, which has been introduced for that purpose from South America. Biological control is, however, a two edged weapon for the animal introduced to destroy some pest may, after doing its duty in this respect, turn its attentions to some other organism which may be of considerable economic importance. Mongeese were brought to the West Indies to rid those islands of the pest of snakes, this they rapidly did but only to become eventually a greater pest than the snakes.

We are experiencing at the present time the effects, and unfortunately only the early effects, of an undesirable importation into this country. In 1905 a few muskrats were imported from North America into

Central Europe with the intention of establishing farms of these animals which produce the valuable musquash fur. Some of these animals escaped and now the muskrat population of Central Europe probably exceeds one hundred million. Despite this example, the same thing has been allowed to happen in this country and this animal is now rapidly establishing itself, notably in the upper reaches of the Severn. The muskrat is really a very large water rat and excavates burrows in the banks of rivers and canals. Herein lies its danger for these burrows are seldom perceived until the bank has become honeycombed with them and has collapsed. Carnivorous mammals which might attack the muskrats have been so greatly reduced in Great Britain that they constitute no check whatsover, and there seems little doubt that this pest will spread far and wide through the country with consequent destruction to waterways. Another animal which has been introduced into England of recent years is the North American grey squirrel. This spread rapidly at first and there seemed some likelihood that it would destroy our native red squirrel, but its early increase has now been stayed and it appears to be settling down as a normal member of the fauna.

Instances of this character, illustrating the far-reaching effects of any interference with the balance of nature, could be multiplied almost indefinitely. But there are instances of animals suddenly increasing in numbers, often at regular periods, which indicate that nature may, on occasion, tend to lose its balance. For centuries past the inhabitants of Norway have been

amazed and mystified by the appearance of vast numbers of little rodents called lemmings which, about every four years, migrate from the interior down to the sea shore where they plunge into the water and are drowned. More recently it has been found that the Canadian lemming increases from time to time in the same way and that this has an important bearing on the fur trade, the Arctic fox, one of the most valuable of fur-bearing animals and which feeds on the lemmings, being always trapped in greatest numbers during such ' lemming years '. Plagues of field mice occur regularly in Europe, while cockchafer beetles are abnormally abundant every four years and in the intervening years often difficult to find. In the sea also the population varies. In one year the spawning of the herring will give rise to an immense new generation, then for a series of years only a minute proportion of the eggs laid will develop into adult fish. The herring fishery in consequence is dependent for a series of years on one good ' year class ' before another comes along, and if this is delayed until the results of the previous good year have been seriously depleted, the stocks of herrings fall very low with disastrous results to the fishery.

Occasionally some change in conditions may enable an animal to extend its distribution. This brings us back once again to the shipworm. Between the years 1914 and 1920 a species, *Teredo navalis*, succeeded in establishing itself in San Francisco Bay. It has previously failed to do so, though it must have been present in the timbers of many ships which entered the

harbour, because there was too much fresh water in the bay. During these years, however, the amount of fresh water brought down by the rivers was abnormally low and the salinity in the bay rose so high that the shipworm was able to live in the water. It quickly made its way into pier piles and other wooden erections in the harbour and these quickly collapsed. Damage estimated at more than ten millions of dollars was done.

In other cases the original causes of the extension in distribution may be as obscure as the results are far-reaching. Some eight hundred years ago the old English black rat invaded this country. Its original home was, apparently, in the forests of the Far East. This animal lives and breeds in houses and always in close contact with man. It is a host of the flea which carries the bacillus of the dreaded bubonic plague, and the succession of terrible plagues which swept Europe from the time of the Black Death to the Great Plague of London in 1665, can all be traced to this rat.

About the beginning of the eighteenth century the second act opens. The brown rat appeared. This animal, larger and hardier than its forerunner, suddenly swarmed into Europe, advancing westward from its home in the plains of Central Asia. In 1727 the waters of the river Volga were seen to be black with hosts of migrating rats. The black rat everywhere gave way before the attacks of the invader and in the course of a century was almost wiped out, surviving only in ships and in the top floors of warehouses in the

neighbourhood of docks where alone its climbing powers gave it an advantage.

The brown rat had no liking for man. It was hardier and could live in the open and away from the warm houses of man, preferring ditches, hay ricks, sewers or slaughter-houses. The friendly black rat had been replaced by the ferocious and suspicious brown rat but bubonic plague disappeared, for though the brown rat harbours the same fleas as the black rat it seldom allows these to transfer themselves to man and so infect him with plague.

Such appeared to be the end of the drama until, during recent years, a third act began to be played. The brown rat, which certainly does untold damage, has been denounced as a pest which must be exterminated. New factories have been built with rat-proof basements, and many of the modern regions of London and other big cities have to a large extent been cleared of these rats. But the chamber, swept and garnished with such care and at such a great expense, has not been kept vacant. The black rat, its great enemy removed, is increasing and is already the commonest rat in certain parts of London. Not only has its ancient enemy been destroyed but man has kindly provided roof kitchens, sky-lights and telephone wires. The black rat has returned with alacrity to the habits of its arboreal ancestors and passes from roof to roof by wires and cables. Up to the present it is abundant only in those parts of London where few people live at night but should the campaign against the brown rat ever allow its rival again to invade in force the

homes of man, particularly near docks where incoming vessels may bring infected black rats, the risk of new outbreaks of plague will be very grave. It seemed so obvious a measure to exterminate the destructive brown rat ; only a knowledge of the place it fills in the economy of nature reveals that it is actually our greatest safeguard against a terrible disease.

It has only been possible here to give the very barest outline of a very important aspect of biology and one, moreover, which must continue to loom larger and larger as man continues the attempt, particularly in the tropics, to force his will regardless of consequences on the animal and plant population. But the study of the economics of nature, for so ecology has aptly been described, is necessary not only for the guidance of man in his dealings with nature but also for the full and proper understanding of life. Just as the many mechanisms of the individual animal are studied in terms of the needs of the animal which possesses them, so must the individual animal, or rather the species to which it belongs, be studied in terms of nature as a whole.

EPILOGUE

A BRIEF summary of modern views on the nature of life forms the most fitting conclusion to this book. The one great thing that we do know for certain about living matter is that all its infinitely diverse representatives had a common origin. Although nothing could be clearer than the distinctions between living and non-living matter, of the essential nature of the former we are almost completely ignorant.

During the nineteenth century biologists were divided into two schools. There were mechanists, who believed that living matter was ultimately explicable in terms of chemistry and physics and that a living thing was essentially an animated piece of mechanism, and on the other hand there were vitalists who postulated the presence of some 'vital force', characteristic of living matter alone, which was responsible for its peculiar properties. While the mechanist regarded the difference between living and non-living matter as one of degree only, the vitalist considered it the distinction between two entirely unlike things. The one disposed of the difference by denying its existence, the other thought he had explained it by evoking some mysterious force incapable of experimental proof.

At the end of the last century the mechanist appeared to be having quite definitely the best of the battle. One by one the outworks of the vitalist position had successfully been stormed. Organic

compounds had been synthesized, the law of the conservation of energy had been proved as applicable to living as to non-living systems, the nature of the digestive processes and of other mechanisms of living matter had been elucidated. The present century has seen many further advances which are acclaimed by the mechanists, such as the tracing out of the complex series of chemical reactions involved in muscular activity, the experimental analysis of inheritance and, above all, the study of conditioned reflexes. The last of these is claimed in certain quarters as but the first stage in the complete analysis of the mental processes which would involve the abolition of the distinction between body and soul, between mind and matter, established by Descartes in the seventeenth century, and so involve the final, irrevocable defeat of the vitalists.

But just when it seemed likely that the mechanists would triumph, battle was joined on a new front. The place of the vitalist has to a large extent been taken to-day by a group of biologists, some of them physiologists, who consider that life *cannot* be explained, that it could not have arisen mechanically, and that, in short, it must just be accepted as a fact. Great stress is laid on the co-ordination of functions so characteristic of life. In the words of J. S. Haldane,[1] "Biology as a science starts from the conception of life itself, and traces in all directions and without spacial limit the co-ordination which life implies. Biological explanation is simply the tracing of the co-ordination as such

[1] See *Materialism* by J. S. Haldane.

in its manifold manifestations." The importance of organization in living matter has been emphasized by others who are particularly concerned with showing that the living organism is something much more than the sum of its parts, and that no amount of analysis can hope to explain the whole.

There is a great deal more to be said in favour of this standpoint than there ever was for the cruder forms of vitalism. At the same time it is, from the point of view of the working biologist, far from satisfactory. He conducts his research with the belief—if not consciously then unconsciously—that he is thereby assisting in the eventual elucidation of the nature of life. Moreover probably no scientist, in the depths of his mind, willingly accepts the belief that the gulf between the living and the non-living can never be bridged, and that science must always deal with two kinds of matter.

Yet, despite all the triumphs of physiology and of genetics, we seem essentially no nearer to the interpretation of living matter. One by one the various mechanisms it employs are studied and explained, but the nature of life itself remains obscure. The analysis of the simplest cell is far beyond the powers of the most skilled chemist. The chemistry of development, involving long series of most complicated reactions, each one, it must be assumed, being set in motion by its predecessor and, in its turn, starting the next, is something quite outside the experience of the chemist and, though he may fully understand the various steps, as a whole, inexplicable.

It is possible that before the nature of life can be elucidated and living matter brought into line with non-living matter some new concept will have to appear. The concepts which have so far emerged from the study of physics and chemistry, though they may be adequate for the explanation of the mechanisms of life, show little sign of providing the explanation of life itself and of its first appearance. The notion of organism or of, wholeness, which shows signs of arising in biology may, if it proves capable of experimental proof, supply this concept. Should this be so biology may prove not only to have enriched itself but also all branches of science for one of the outstanding results of modern physical research has been the collapse of the idea of particles, and many eminent physicists have stated their belief in the necessity of some new concept of organism.

It seems improbable that such a development will come from the study of physics. It is to biology that we may reasonably look for the next great advance in science, an advance which may make possible, by the elucidation particularly of mind, the final explanation of living matter, and also lead to the culminating unity of science by the reconciliation of biology and physics.

BOOKS FOR FURTHER READING

THE following books, many of which have been referred to in footnotes, have been selected because they are, in the main, addressed to the general reader and deal with aspects of biology particularly emphasized in this book.

GENERAL BIOLOGY

J. B. S. HALDANE and J. HUXLEY: *Animal Biology.* Clarendon Press.

E. S. GOODRICH: *Living Organisms.* Clarendon Press.

A. E. SHIPLEY: *Life.* Cambridge University Press.

F. KEEBLE: *Life of Plants.* Clarendon Press.

J. B. S. HALDANE: *Possible Worlds.* Chatto and Windus.

J. B. S. HALDANE: *The Inequality of Man.* Chatto and Windus.

J. HUXLEY: *Essays in Popular Science.* Chatto and Windus.

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